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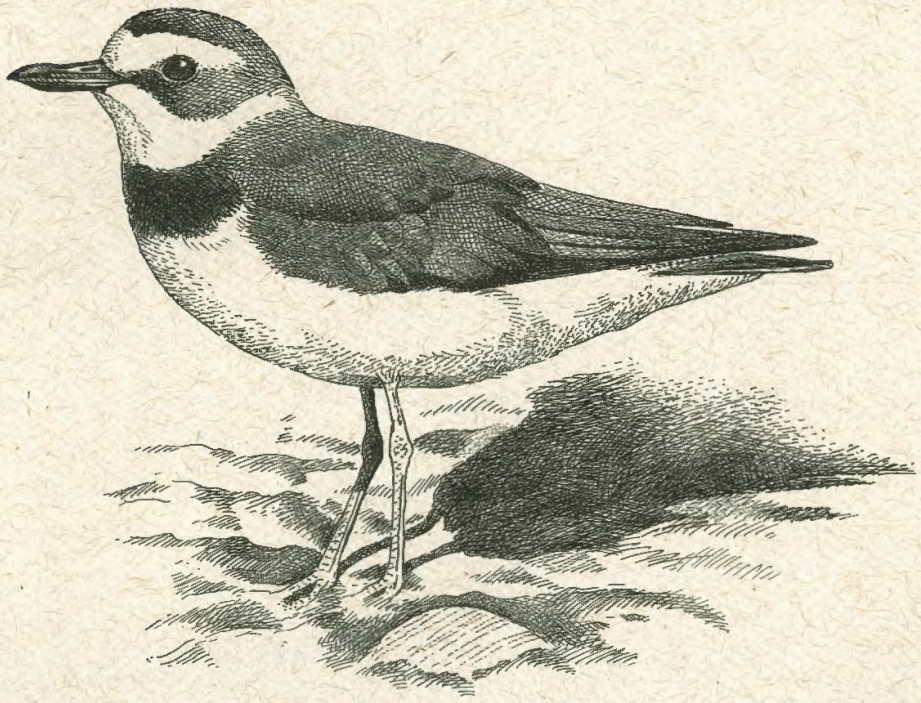

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COVER: Wilson's Plover (*Charadrius wilsonia*). Illustration by Don Radovich.

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FRONTISPIECE. Cliff Swallow (*Petrochelidon pyrrhonota*) exhibiting typical vigilance at its nest in a southwestern Nebraska breeding colony (see Roche and Brown, pages 685–695). Individuals vary in the extent to which they are vigilant, and these individual differences may reflect different personality types. Photograph by Charles R. Brown.

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AMONG-INDIVIDUAL VARIATION IN VIGILANCE AT THE NEST IN COLONIAL CLIFF SWALLOWS

ERIN A. ROCHE[1,2] AND CHARLES R. BROWN[1]

ABSTRACT.—Enhanced vigilance against predation is often an advantage of living in groups, but most studies have not examined individual-specific variation in the propensity to be vigilant among the animals within a group. We studied vigilance at the nest in colonially nesting Cliff Swallows (*Petrochelidon pyrrhonota*) in southwestern Nebraska in 2011 and 2012, and asked whether differences among individuals were consistent over time, whether vigilance varied among different colonies, and whether there were positive or negative fitness consequences of different levels of vigilance. We found significant among-individual variation in extent of vigilance and some variation among different colony sites. Vigilance also varied with date and nesting stage, but other phenotypic characteristics of a bird had no effect on vigilance. Differences among individuals in vigilance were not strongly related to their reproductive success that season, but more vigilant individuals were more likely to attempt intrusions into their neighbors' nests. Vigilance at the nest may be partly directed at monitoring conspecifics' activities in neighboring nests. This study is among the few that have investigated individual variation in vigilance behavior, a possible index of personality for Cliff Swallows, and the first to measure variation in vigilance for a colonial bird while breeding. *Received 31 December 2012. Accepted 2 March 2013.*

Key words: coloniality, personality, *Petrochelidon pyrrhonota*, reproductive success, social behavior, vigilance.

One major challenge facing most animals is allocating time between predator-directed vigilance and mutually incompatible activities such as foraging, courting, or caring for offspring. Many studies have examined correlates associated with individual vigilance, finding that investment in vigilance often varies with age, sex, dominance, reproductive stage, distance to cover, position in a group, predation pressure, and, perhaps most commonly, group size (reviewed in Elgar 1989, Carter et al. 2009). Because the probability of detecting a predator is generally greater in larger animal groups (Pulliam 1973; Hoogland 1979, 1981; Hart and Lendrem 1984; Brown and Brown 1987; Roberts 1996), it is widely believed that sociality often affords the twin advantages to an individual of reducing both predation risk and the investment it must personally make in being vigilant.

The extent to which a given individual within a group experiences the benefit of being able to allocate less time to vigilance depends largely on context. However, it is well known that certain individuals are routinely more vigilant than others (Jennings and Evans 1980, Inglis and Lazarus 1981, Lima 1987, Elgar 1989), and this implies that vigilance-related advantages apply unequally to animals within a group. Theoretical studies

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TABLE 1. Observation effort for vigilance studies of Cliff Swallows at four colonies, showing the total number of swallows observed (*n*), the total number of focal observations of individuals conducted at each colony, the colony-specific mean and standard deviation (SD) of the number of focal observations conducted per individual, and colony size (number of nests).

Colony site	Year	*n*	Focal observations	Mean (SD)	Colony size
Aquaduct	2012	10	23	2.3 (0.8)	20
CR1	2012	39	169	4.4 (1.1)	165
CR1	2011	41	188	4.5 (1.5)	170
Junkyard	2012	26	118	4.4 (1.5)	1,575

have examined how variation in vigilance among individuals within groups influences the link between group size and predator detection (Bednekoff and Lima 2002, Michelena and Deneubourg 2011, Beauchamp et al. 2012). Behavioral differences among animals that are consistent over time are recognized as animal "personalities" (Réale et al. 2000, Dingemanse et al. 2002, Carere et al. 2005, Réale and Dingemanse 2010), and individual personality traits such as aggressiveness or boldness may be correlated and make up a "behavioral syndrome" (Sih et al. 2004a, b; Bell and Sih 2007).

Empirical studies of individual variation in vigilance behavior are relatively scarce. For example, many studies on vigilance have been done with unmarked animals, often in large foraging flocks where an individual may be difficult to re-locate, or have specifically excluded multiple observations of the same individual for statistical simplicity (Carter et al. 2009). An exception was a study of lizards, in which individuals varied consistently enough in their response to the risk of predation to suggest that anti-predator behavior could be a distinctive personality trait (Lopez et al. 2005), and perhaps part of a wider behavioral syndrome (Sih et al. 2004a, b; Bell and Sih 2007). Thus, could some of the variation in vigilance among individuals be related to personality, independent of extrinsic factors affecting vigilance?

As in many species that live in groups, anti-predator advantages are important in colonially nesting Cliff Swallows (*Petrocheldion pyrrhonota*). Colony-level vigilance (as reflected in distances at which incoming predators are detected) increases in larger Cliff Swallow colonies (Wilkinson and English-Loeb 1982, Brown and Brown 1987), and enhanced predator avoidance may be one reason these birds form colonies (Brown and Brown 1996). However, despite extensive long-term work on the benefits of coloniality in Cliff Swallows, we know nothing about individual differences in vigilance allocation or the variability in potential vigilance-related advantages for birds in different colonies.

In this study, we examine whether individual differences in vigilance among nesting Cliff Swallows were consistent over time. Our objectives were to identify: (1) whether individual vigilance levels varied among colonies representing very different social environments; (2) whether there were positive or negative fitness consequences of different levels of vigilance; (3) whether vigilance levels were associated with trespassing behavior; and (4) if individual Cliff Swallows formed breeding pairs assortatively with respect to propensity to be vigilant. Consistent individual differences in vigilance would suggest that this behavior could be useful in defining personality types (Réale et al. 2000, Dingemanse et al. 2002, Carere et al. 2005, Réale and Dingemanse 2010), and systematic differences among birds in colonies of different sizes might suggest some degree of phenotypic sorting into groups (Brown et al. 1990; Brown and Brown 2000, 2001; Spottiswoode 2007, 2009) based on personality traits. Unlike in most studies of vigilance, which have been conducted in flocking species in the non-breeding season or away from breeding sites, we were able to study how Cliff Swallows allocate vigilance at their nest while breeding and thus to directly determine how reproductive success varies among individuals who exhibit different levels of vigilance.

METHODS

Study Area.—Cliff Swallows have been studied since 1982 near the Cedar Point Biological Station (41° 13′ N, 101° 39′ W) in Keith County, southwestern Nebraska, USA, along the North and South Platte rivers; the study area also includes portions of Deuel, Garden, and Lincoln counties.

In this area the birds nest mostly on the sides of bridges, in box-shaped road culverts, or underneath overhangs on the sides of cliffs. The breeding season lasts from early May to mid-July. The study area contains about 220 colony sites (i.e., physical structures on which colonies may form), with about a third not used in a given year. Colony size varies widely; in southwestern Nebraska it ranges from 2–6,000 nests (mean ± SE, 404 ± 13, n = 2,318 colonies), with some birds nesting solitarily. The study site is described in detail by Brown and Brown (1996).

Field Methods.—In 2011 and 2012, we captured Cliff Swallows in mist nets at selected colonies as they exited from their nests; see Brown (1998) for capture methods. For individual recognition at a distance, we used permanent, non-toxic Sharpie® markers to apply unique 3- and 4-color stripe combinations to the birds' white forehead patches, which are highly visible when Cliff Swallows are present at their nests (Brown and Brown 1996). We color-marked and observed a total of 116 Cliff Swallows at four colonies; at one site, Cliff Swallows were observed in both years (although not the same individuals), and we considered these two separate colonies (Table 1).

Following marking, we observed each colony to determine at which nests the marked swallows were residents. We created schematic maps of each colony and assigned marked swallows to their nests by watching for repeated nest visits, indications of nest defense, and eventual egg-laying. Once nest assignment was complete, we marked focal nests by painting numbers on the nests' mud exteriors to facilitate observation.

Behavioral observations were conducted primarily by two observers in 2011 and three in 2012. We rotated among the color-marked birds, selecting one at a time to watch as a focal animal. We typically watched a given bird only once per day, and selected individuals for each day's observations based only on how many previous times a bird had been observed. We tried to accumulate an equivalent number of focal-animal watches for all color-marked birds, and had at least 4 for most individuals (mean = 4.2, SD = 1.4). In 2011, observations were conducted from initial nest construction at a colony through egg-laying but were terminated when eggs hatched, while in 2012 we conducted observations until nestlings fledged.

Observers sat as close to nests as possible (typically 2–3 meters from the entrance of the colony) without noticeably influencing the behavior of the birds and conducted 15-min focal observations on color-marked individuals using binoculars. During a focal observation, we recorded the behavior exhibited by the bird during every 15-sec interval, not watching any other bird during that time. This included noting whether the individual was present at the nest entrance, out of sight inside the nest, absent from the colony, interacting with neighbors, or nest-building. Vigilance was defined as a bird being visible in the tubular entrance of its nest, peering out. Birds out of sight inside the nest were considered not vigilant. Sitting in the nest entrance precluded incubating eggs or brooding young, given the gourd-shaped architecture of a typical cliff swallow nest. Any focal individual that left its nest and attempted to enter a neighboring nest (a trespass attempt, as described by Brown and Brown [1996]) was so noted.

We conducted nest checks beginning, prior to, and during, nest initiation at the nests of the focal individuals, using a dental mirror and flashlight inserted through the nest's tubular mud neck. Nests were checked at 2–4 day intervals throughout the nesting season to monitor laying times, hatching dates, and nestling presence. At 17 days after the estimated hatching date, the number of nestlings surviving in each nest was determined, and we used this metric as a relative estimate of annual reproductive success for each color-marked bird. Although Cliff Swallows typically fledge at 23–26 days (Brown and Brown 1995), premature fledging can occur if mirrors are inserted into nests after nestlings reach 17 days of age.

The colonies used in this study were fumigated to remove ectoparasites approximately once a week, as described by Brown and Brown (1996). Cliff Swallow colonies of different sizes vary widely in the numbers of blood-sucking swallow bugs (Hemiptera: Cimicidae: *Oeciacus vicarius*) infesting the nests, and bugs represent a major source of nesting failure that tends to increase with colony size and swamps the effects of other independent variables (Brown and Brown 1996). Fumigation eliminated ectoparasitism as a confounding factor on reproductive success, although because parasite load has been implicated as a potential cause of individual variation in behavior (Barber and Dingemanse 2010, Kortet et al. 2010), we acknowledge that we possibly affected among-individual variation in vigilance by fumigating nests. Under these conditions, we would expect any

individual variation we detect to be a conservative measure.

Statistical Analyses.—We scored vigilance for each bird by tabulating the total number of 15-sec increments during which a swallow was observed being vigilant for each 15-min focal observation period. If a swallow was observed doing more than one activity within a 15-sec interval, we weighted that interval by the number of different activities that individual was engaged in. We log transformed these values to use as a response variable in linear mixed regression models (LN [vigilance + 1]). We considered these values an index of an individual's propensity to be vigilant.

We used linear mixed models to assess whether there was significant variation among individuals by including the identity of each individual as an intercept-only random effect (ID). The unique intercept differences between individuals can be interpreted as among-individual differences in behavior (Betini and Norris 2012, Dingemanse and Dochtermann 2013). Similarly, as each individual was associated with a specific colony, we included colony as an intercept-only random effect (Colony). Statistical support for a random effect of colony would indicate some of the residual variance in vigilance behavior was also explained by among-colony differences (Dingemanse and Dochtermann 2013). As multiple 15-min observation periods were conducted on any given day, we controlled for among-day differences in behavior by also including a random effect of Julian date (Date).

Although we were primarily interested in whether there were differences in vigilance behavior among individuals (i.e., support for ID) and colonies (i.e., support for Colony), we also controlled for other environmental and demographic factors that could influence Cliff Swallow behavior. To do this, we built a full model consisting of all covariates we believed might be important (treated as fixed effects; Table 2) and, beginning with the full model, used a process of backward selection in which we sequentially removed each covariate. We evaluated each model with its Akaike's Information Criterion corrected for small sample size (AIC_c) and accepted the removal of a covariate if its deletion resulted in a lower AIC_c value (Burnham and Anderson 2002). We conducted statistical analyses using program R (R Development Core Team 2012), fit general linear mixed models using package "lme4" (Bates et al. 2012), and calculated AIC_c using the package "AICcmodavg" (Mazerolle 2012).

For linear models of vigilance, we used an (exact) restricted log likelihood ratio test (RLRT) to test whether the variance of a random effect deviated from 0; the RLRT test was fit using the exactRLRT function in the RLRsim package (Sheipl et al. 2008) on the top model that controlled for all relevant fixed effects. We used the RLRT test to investigate whether there was support for significant differences between individuals (i.e., support for the random effect of ID; *sensu* Betini and Norris [2012]). To determine the extent of variation in vigilance explained by the individual, colony, and date, we also calculated repeatabilities for our top model following Dingemanse and Dochtermann (2013; and see Lessels and Boag [1987], Nakagawa and Schielzeth [2010]).

To examine the relationship of vigilance to reproductive success, we extracted conditional modes of the ID random effect from the linear mixed model for use as vigilance scores (Boon et al. 2007, Martin and Réale 2008, Betini and Norris 2012). These conditional modes (or BLUPs, best linear unbiased predictors) predict the random effect term independent of other potentially confounding terms in the linear mixed model (Pinhero and Bates 2000). We hereafter refer to these values as an individual swallow's relative vigilance score. We examined the relationship between reproductive success and vigilance scores using a correlation.

We were similarly interested in whether an individual Cliff Swallow's propensity to trespass might be associated with its vigilance level. We used a Wilcoxon rank-sum test to compare the vigilance scores (represented by the BLUPs) for individuals that had been observed trespassing at least once ($n = 18$ individuals) to those individuals that had never been observed trespassing ($n = 98$ individuals).

To assess whether assortative mating by vigilance was occurring, we conducted a two-tailed random permutation test (coded in program R) to compare the difference in mean relative vigilance score (as measured by the vigilance BLUP) within a mated pair ($n = 13$ mated pairs) to the difference in mean relative vigilance score within randomly paired individuals that were not part of a mated pair in which behavioral observations were made on both individuals ($n = 4{,}005$ remaining permutations). The difference in the means between these two groups was taken (e.g., $T_{obs} = \bar{x}_{matediff} - \bar{x}_{randiff}$). The within-pair differences in vigilance scores for the two groups

TABLE 2. Covariates included in linear mixed-effects models to explain vigilance in Cliff Swallows.

Covariate	Effect	Type	Definition
Age	Fixed	Continuous	Relative age of the focal bird, taken as observation year minus banding year + 1 for birds banded as adults; observation year minus banding year for birds banded as juveniles.
Experience	Fixed	Categorical	Whether or not the focal bird was known to have nested at its colony site in a previous year (only known for birds first banded in a previous year).
Absence	Fixed	Continuous	Total amount of time a swallow was absent during a 15-min focal observation (LN + 1 transformed).
Stage	Fixed	Categorical	Whether the nest of a focal bird had eggs or nestlings on a given date.
Sex	Fixed	Categorical	Sex of the focal bird.
Mass	Fixed	Continuous	Body mass of the focal bird relative to other birds caught at the same site on the same date and of the same sex.[a]
Colony	Random *(intercept)*	Categorical	Colony where bird was resident.
Date	Random *(intercept)*	Categorical	Julian date on which an observation occurred.
ID	Random *(intercept)*	Categorical	Focal individual (ID = band number)

[a] Mass was standardized using the mean body mass of all birds of the same sex caught at the same colony on the same day (i.e., $mass_{standardized} = (mass_{individual} - mass_{mean})/mass_{SD}$).

were pooled (n = 4,018) and a sample of 13 was randomly drawn from the pooled group without replacement, and the mean of this sample was taken. The mean of the random sample was subtracted from the mean of the group without the sampled individuals, and the process was repeated over 10,000 iterations. P-values were generated by summing the permuted absolute value of the differences $\geq$ the absolute value of T_{obs} and taking the mean (Roche et al. 2008).

RESULTS

We found support for individual differences (the ID random effect) in vigilance after controlling for other environmental covariates associated with behavioral variation (Table 3). The random effect of ID used in our linear mixed models for vigilance behavior was significant using an (exact) restricted log-likelihood test (RLRT = 7.42, P = 0.003 based on 116 individuals and 10,000 simulated values). However, the associated biological repeatability score for among-individual variance, which is a measure of how much of the variation in vigilance behavior is accounted for by the individual (i.e., ID), and thus how different individuals were from each other across the study area, was low (Repeatability = $V_{ID}/(V_{ID} + V_{Colony} + V_{Date} + V_{Residual})$ = 0.067; Table 3). On a given day and within a given colony, the repeatability of an individual's behavior was slightly higher (Repeatability = $V_{ID}/(V_{ID} + V_{Residual})$ = 0.089). The amount of vigilance behavior a Cliff Swallow displayed was also explained in part by the amount of time an individual was present at its nest (i.e., those more frequently absent were less vigilant when they were present; Table 3) and stage of reproduction (i.e., birds were more vigilant when incubating eggs than when raising nestlings; Table 3). Age, body mass, sex, and experience had no effect on vigilance, as these covariates were eliminated from the final model based on AIC_c scores.

We found some evidence of among-colony differences in vigilance of Cliff Swallows using the (exact) restricted log-likelihood test (RLRT = 2.192, P = 0.036 based on 116 individuals and 10,000 simulated values), but biological within-colony repeatability, in this case how different the behavior at different colonies was across the study area, was similarly low (Repeatability = $V_{Colony}/(V_{ID} + V_{Colony} + V_{Date} + V_{Residual})$ = 0.029). The colony that was associated with the least amount of vigilance behavior was CR1 in 2012 (BLUP = −0.186 ± 0.106 SE) and the site with the most vigilance behavior was CR1 in 2011 (BLUP = 0.136 ± 0.129 SE). However, the differences in the (transformed) raw vigilance scores among colonies were not obviously related in any way to colony size (Fig. 1).

The number of nestlings surviving to day 17 in nests of the more vigilant birds (i.e., individuals with higher relative vigilance scores) was slightly

TABLE 3. Regression coefficient estimates and standard errors (SE) for fixed effects and variance estimates for random effects from the top linear mixed model (selected via backwards selection and minimum AIC_c value) used to explain variation in vigilance among Cliff Swallows. We calculated the "true biological repeatability" of our sample following Dingemanse and Dochtermann (2013). For example, the repeatability of the random effect of individual was calculated as: $V_{ID}/(V_{ID} + V_{Colony} + V_{Date} + V_{Residual})$ where "V_{ID}" is the phenotypic variance attributed to the individual and $(V_{ID} + V_{Colony} + V_{Date} + V_{Residual})$ is the cumulative phenotypic variance of the sample explained by the random effects.

Regression coefficient:	Random effects variance	Repeatability
ID (intercept) [a]	0.083	0.067
Colony (intercept) [b]	0.035	0.029
Date (intercept)	0.298	0.242
Residual	0.814	0.662
	Fixed effects estimates	
Stage (egg)	1.568 (0.169 SE)	-
Stage (chick)	1.220 (0.205 SE)	-
Absence	−0.125 (0.033 SE)	-

[a] RLRT = 7.42, $P = 0.003$ based on 116 individuals and 10,000 simulated values.
[b] RLRT = 2.192, $P = 0.036$ based on 116 individuals and 10,000 simulated values.

lower than that for the less vigilant individuals, although the relationship was not statistically significant at the $P = 0.05$ level ($r_s = -0.16$, $P = 0.08$, $n = 116$ birds, Fig. 2).

There was an association between vigilance and the probability of trespassing into a neighboring Cliff Swallow's nest: the mean (± SE) relative vigilance score for birds ($n = 18$) seen to trespass

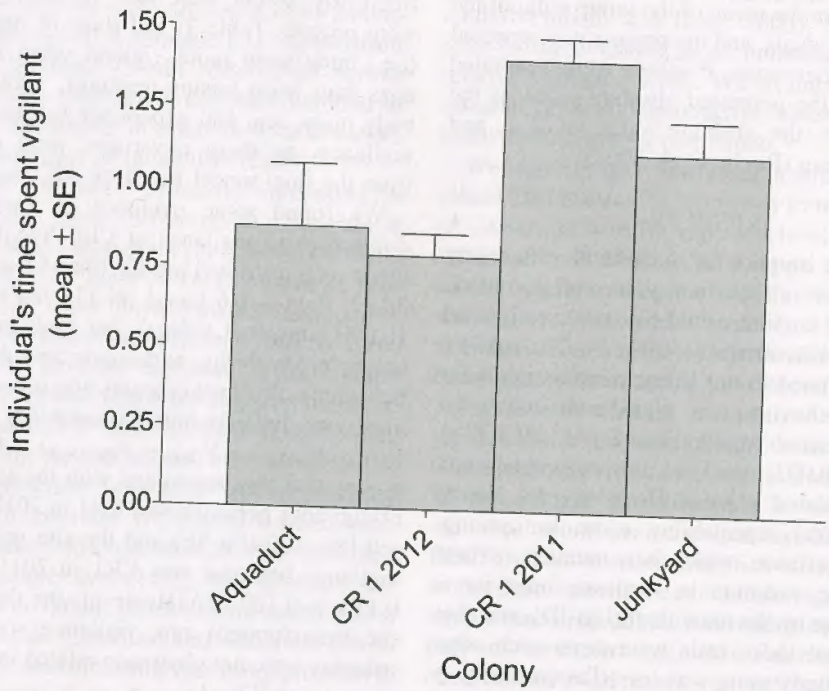

FIG. 1. The frequency with which an individual Cliff Swallow was vigilant at the nest (the natural log-transformed amount of time the bird was vigilant during a 15-min focal observation period) in relation to the colony in which it was resident. Means (± SE) for all birds at a site are shown; sample size (number of individuals observed) and colony size for each site are given in Table 1.

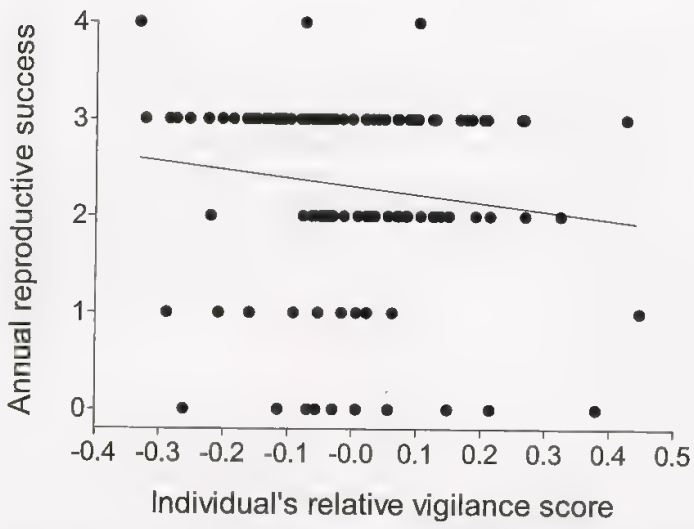

FIG. 2. Annual reproductive success (number of nestlings surviving to 17 days of age) of Cliff Swallows in relation to an individual's relative vigilance score. Higher scores indicate increased vigilance. Vigilance scores are represented by the conditional modes (BLUPs, best unbiased linear predictors), which described the random effect of individual, independent of other fixed effects in the top linear model (Pinheiro and Bates 2000). Reproductive success declined with vigilance score but was not significant ($r_s = -0.16$, $P = 0.08$, $n = 116$ birds). Line indicates best-fit least-squares regression.

elsewhere at least once (0.105 ± 0.038) was over 5 times that of the scores for individuals ($n = 98$) never seen to trespass (-0.020 ± 0.014), and the difference was significant (Wilcoxon test, $Z = 3.03$, $P = 0.002$).

There was some suggestion that vigilance of Cliff Swallows in mated pairs was more similar than vigilance among randomly generated pairs, although our sample size of mated pairs was small ($n = 13$) and the trend not significant at the $P = 0.05$ level (two-tailed permutation test, $P = 0.10$).

DISCUSSION

Our study revealed significant among-individual and among-colony variation in nest-site vigilance exhibited by Cliff Swallows. Vigilance varied with date and nesting stage, but other phenotypic characteristics of a bird (e.g., sex, age, and experience at a site) had no effect on vigilance. Differences among individuals in vigilance were not significantly related to their reproductive success that season, but more vigilant individuals were significantly more likely to attempt intrusions into their neighbors' nests. This study is among the few that have investigated individual variation in vigilance behavior (Carter et al. 2009, Rieucau et al. 2010, Couchoux and Cresswell 2012), and the first to measure variation in vigilance for a colonial bird.

Behavioral syndromes consisting of a constellation of co-occurring personality traits are now well known in many species (Sih et al. 2004a, b; Dingemanse and Wolf 2010). In other species in which significant among-individual differences in anti-predator behavior have been demonstrated, it was suggested that these differences reflect a "shy-bold" continuum in personality types (Lopez et al. 2005). Although our data support the existence of a personality based on vigilance, it remains unclear whether this vigilance is the same as boldness. For example, more vigilant Cliff Swallows were also more likely to trespass at neighboring nests, indicating that the vigilant personality type may be more likely to take risks (i.e., evidence of boldness) and is also more aggressive. Trespass attempts often end in violent fights in which the trespasser is repelled when a neighbor is present in the nest that is invaded (Brown and Brown 1996). Because they presumably can better monitor what is occurring in or near the colony than can birds that are out of sight in the nest, more vigilant individuals probably have better information to judge whether a disturbance to the colony merits vacating the nest. If a bird remains at the colony in the face of imminent threat from a terrestrial predator such as a snake, it could be considered bold, especially since snakes do prey on adult Cliff Swallows in

their nests (Brown and Brown 1996). However, an individual fleeing its nest in the presence of an aerially hunting raptor approaching the colony could also be considered bold, in that it enhances its risk of being attacked as it exits the site. Thus, context is important in knowing whether a given behavior could be considered bold versus shy.

As in most studies of vigilance, we could not rule out that some of the vigilance exhibited by Cliff Swallows at their nest was directed at conspecifics instead of at potential predators. Vigilance in many species may also reflect social interactions with group members, such as in competition for mates or looking for food (Burger and Gochfeld 1988, Beauchamp 2001, Robinette and Ha 2001, Carter et al. 2009). In Common Redshanks (*Tringa totanus*), individuals have been observed to adjust their vigilance level depending on the riskiness of the situation with varying degrees of plasticity (Couchoux and Cresswell 2012). The fact that high levels of vigilance in Cliff Swallows frequently led to trespass attempts supports the view that birds scanning at their nest may be monitoring their neighbors, looking for a nest to intrude upon. However, the vigilant birds at their entrances were also the first ones to give alarm calls if a predator managed to enter the colony undetected by swallows flying overhead, and the vigilant birds were the first ones to exit (C. R. Brown, pers. obs.). Being vigilant was presumably beneficial in allowing a bird to be among the first wave of residents flying out of the colony.

We found a weak association between individual vigilance and reproductive success in Cliff Swallows. The more vigilant swallows tended to rear fewer nestlings to approximate fledging age (Fig. 2). The lack of statistical significance of this relationship may have reflected in part our relatively small sample size ($n = 116$ individuals) for demographic studies, meaning that we could detect only rather large changes in reproductive success associated with vigilance. Additionally, our use of fumigated nests for this study might have diminished variability in observed reproductive success and reduced our ability to detect a link between vigilance and fitness.

Vigilance-related fitness trade-offs have been previously documented in Gray Partridges (*Perdix perdix*; Watson et al. 2007). For this species, increased vigilance levels were associated with lower winter survival even when flock size was controlled, suggesting vigilance behavior had long-term costs perhaps as a result of increased starvation risk (Watson et al. 2007). If, as our data suggest, vigilance in Cliff Swallows is associated with a fitness cost such as diminished annual reproductive success, it may be because the more vigilant individuals are more likely to leave their nests unattended while trespassing elsewhere, potentially making their own nests more vulnerable to interference from neighboring conspecifics that may destroy eggs (Brown and Brown 1988, 1996). Also, the more vigilant individuals might have more inconsistent incubation and poorer provisioning of young: perching at the nest entrance precludes incubating eggs or foraging for food for nestlings, and in Cliff Swallows both parents incubate and feed the young. This effect could be potentially exaggerated if swallows are more likely to mate assortatively based on proclivity to be vigilant (and trespass), which our data suggest.

Behaviors such as aggression and boldness have been linked to degree of sociality in some birds (Verbeek et al. 1999, Fox et al. 2009, Kurvers et al. 2009, David et al. 2011), and the same may be true, at least in part, for vigilance in our study. The social environment as represented by the colony site was associated with the level of vigilance a Cliff Swallow exhibited, although there was a relatively small difference in individual vigilance among colonies. This result is somewhat surprising given that the colony sizes (and thus the social environments) of the Cliff Swallow colonies we studied were quite different, with these colonies varying in size by almost two orders of magnitude. One colony, Aquaduct, was small, and birds there rarely interacted in general and by trespassing in particular, perhaps because the nests were far apart (making it more difficult to perhaps impossible for swallows to see what their neighbors were doing). In contrast, Junkyard was a massive colony where nests occurred in high density, with most nests physically touching four or more adjacent ones. If vigilance at the nest is directed primarily at predators, we might expect the most vigilance among birds at Aquaduct and the least at Junkyard, following the group-size effect so pervasive among most studies on flocking animals.

That we did not see these predicted differences may reflect the fact that vigilance at one site (the small colony) was directed primarily at predators and at the other (the large colony) primarily at the

many neighboring conspecifics, including for the gathering of information about foraging success (Brown 1986). Such behavior would not be unprecedented. Results from a study on vigilance in eastern grey kangaroos *(Macropus giganteus)* suggested that the increased vigilance towards conspecifics exhibited by some individuals in larger group sizes could offset the reduction in anti-predator vigilance exhibited by others (Carter et al. 2009). Higher levels of conspecific-directed vigilance in larger groups may often obscure the predicted vigilance-group-size relationship in general (Beauchamp 2001).

Could Cliff Swallows sort among colony sizes based on vigilance and shy-bold personality types? While other evidence suggests that these birds are non-randomly distributed among different colony sizes (Brown and Brown 1996, 2000; Brown et al. 2005), results of this study do not indicate a simple relationship between vigilance and colony size. Experimental manipulation would be necessary to determine if the small (but significant) differences in vigilance between colonies are a result of phenotypic sorting of some sort, or a result of the colony environment and how it affects the behavior of the swallows. For example, inherently more vigilant individuals might settle in smaller colonies, or small colonies may cause the birds who settle there (for other reasons) to be more vigilant. When group size was experimentally manipulated for wild-caught Scaly-breasted Munias (*Lonchura punctulata*), rank individual differences in vigilance were retained, and individuals appeared to respond to increasing group size equivalently (Rieucau et al. 2010). Clearly, a similar mechanism could be at play for Cliff Swallows, with average vigilance levels a product of context (Couchoux and Cresswell 2012). The relatively small number of colonies we studied (four) dictates caution in making conclusions about vigilance behavior and colony size, but the fact that there were so few differences in vigilance behavior over the wide colony-size range indicates that extension of these laborious observations to additional colonies likely would not change our conclusions.

Cliff Swallows have expanded their range in much of North America since the 1960s in response to construction of bridges and culverts (Brown and Brown 1995), and in many areas these birds have adopted locally novel nesting substrates such as buildings of particular types or circular metal drainage tubes. Who are the individuals that are the first to find these new sites? Are they substantially different from those swallows that have continued to nest on cliff faces or that show higher fidelity to established colony sites? Perhaps they differ in vigilance, aggressiveness, or an as yet unmeasured exploratory personality. Continued study of the behavioral profiles that allow some individuals, but not others, to successfully transition from one breeding environment to another would contribute to our understanding of why animal personalities persist and also have implications for conservation of species that have proved to be less environmentally flexible.

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WITHIN-SEASON NESTING DISPERSAL AND MOLT DISPERSAL ARE LINKED TO HABITAT SHIFTS IN A NEOTROPICAL MIGRATORY SONGBIRD

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ABSTRACT.—Dispersal decisions of songbirds are relatively well understood between breeding seasons, but far less is known about dispersal between nesting attempts and during the molting period. There are several non-mutually exclusive hypotheses for why birds disperse during breeding and molt including: (1) avoiding predation, (2) because of depleted resources, or (3) seeking higher quality habitat. In this study, we evaluated the above hypotheses by radio-tracking a Neotropical migrant, the Wood Thrush (*Hylocichla mustelina*), during breeding and molt. During breeding, 30% (7/23) of females moved territories within-season. Females were not more likely to move off-territory following nest predation, and dispersing females were not in poorer nutritional state than non-dispersing females prior to the move. However, females occupying nest sites with large trees, high canopy height and percent canopy cover, and low percent ground cover were more likely to move off-territory for their second nest to sites with few large trees, a low canopy height and cover, and high percent ground cover. During the molting period, 61% (28/46) of birds moved off-territory to molt. Molting areas were associated with more shrubs and fruiting trees compared with breeding territories. There were no sex or age effects as to whether a bird molted on or off their breeding territory. We suggest that off-territory movements during the nesting period are to seek more suitable nesting vegetation, rather than specifically avoiding predation or because of reduced resource availability. This study has additionally shown that, without radio-telemetry, detecting off-territory movements during breeding is difficult and neglecting to include these movements may result in an underestimation of annual productivity.
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Key words: dispersal, *Hylocichla mustelina*, molt, molt habitat, nesting habitat, plasma lipid metabolites, Wood Thrush.

Within-season breeding dispersal is common in multi-brooded avian species (e.g., Jackson et al. 1989, Howlett and Stutchbury 1997, Powell and Frasch 2000, Grégoire and Cherry 2007), but for most species it is unknown how often within-season dispersal occurs. Additionally, our understanding of movements by songbirds off breeding territories to molting areas has only been thoroughly addressed, to our knowledge, by three studies (Vega Rivera et al. 1999, 2003; Vitz and Rodewald 2007). Without the use of radio-telemetry many studies are unable to quantify within-season dispersal, whether during or after breeding, because it is often difficult to confirm dispersal versus mortality if birds are secretive or travel off the study site (e.g., Vega Rivera et al. 1999, 2003; Powell and Frasch 2000). In this study, we investigate hypotheses for why birds disperse within a breeding season, and why birds move from breeding to molting sites.

Following nest failure or success, females can choose to stay on the same territory with the same mate, move to a new territory with the same mate, or change territories and mates (Jackson et al. 1989). Jackson et al. (1989) proposed several hypotheses and predictions as to why birds disperse between nesting attempts. We focus on the predation and resource availability hypotheses. First, birds may disperse to avoid predation, and thus birds with failed nesting attempts would be far more likely to disperse to an area that was no longer within a predator's home range. The predation hypothesis has been studied extensively and some studies strongly support the hypothesis (Greig-Smith 1982, Grégoire and Cherry 2007), while others do not (Jackson et al. 1989, Beletsky and Orians 1991, Howlett and Stutchbury 1997). One explanation for the discrepancy in the results of previous studies is movements between nesting sites could be related to predator home ranges such that re-nesting birds, whether they had been successful or not, select habitat where predation risk is likely to be lower (Jackson et al. 1989, Powell and Frasch 2000). Birds may also move off-territory to upgrade their nesting habitat to areas of lower predator abundances or more suitable nesting habitat with more optimal

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substrate or more food (Tewksbury et al. 1998, Powell and Frasch 2000, Betts et al. 2008).

The resource availability hypothesis (Jackson et al. 1989) has not been thoroughly tested for within season nesting dispersal in birds. However, intrinsic measures, such as measures of fat deposition (plasma lipid metabolite profiles) or corticosterone (CORT) directly measure the nutritional and energetic state of a bird (Jenni-Eiermann and Jenni 1994, Jenni and Jenni-Eiermann 1996) and reflect resource availability. Owen et al. (2005) used plasma lipid metabolites as an indication of food limitation and habitat quality in Willow Flycatchers (*Empidonax traillii extimus*) and suggest that intrinsic measures of nutrition provide a better indication of food limitation than insect density. Thus, by obtaining blood samples one can assess the resource availability hypothesis. If birds are food limited, CORT levels increase which in turn increases the amount of time the birds spend searching for food and consequently, triggers movement behaviors (Wingfield 1994). Additionally, plasma lipid metabolites measure changes in metabolism and provide a direct measure of the nutritional condition of free-living birds (Jenni and Jenni-Eiermann 1996). Plasma triglycerides (TRIG) provide a measure of fat deposition and mass gain, and high triglyceride levels are indicators of a well-fed individual (Jenni-Eiermann and Jenni 1994). When an individual is food restricted, stored TRIG is mobilized which releases free glycerol (GLYC) and free fatty acids in the plasma resulting in an elevation of β-hydroxybutyrate (BUTY; Jenni and Jenni-Eiermann 1996). High levels of BUTY and GLYC are indicators of periods of low food abundances (Jenni-Eiermann and Jenni 1996). Thus, if food abundance was a factor affecting dispersal either during nesting or between breeding territories and molting sites, then we would expect birds occupying areas with low food abundances to have high CORT, low TRIG, and high levels of BUTY or GLYC.

The molting period is a period of high energetic demand (Murphy and King 1992). During molt, individuals become highly sedentary, are sometimes incapable of extensive flight (Holmgren and Hedenström 1995, Vega Rivera et al. 1999), have increased thermoregulation demands (Holmgren and Hedenström 1995), and high physiological demands because of their synthesis of new feathers (Murphy and King 1992). Thus, habitat may play a significant role for molting individuals both in terms of concealment from predators and access to sufficient food resources to fuel feather growth. Vega Rivera et al. (1999, 2003) found that Wood Thrushes (*Hylocichla mustelina*) and Scarlet Tanagers (*Piranga olivacea*) in Virginia had different habitat requirements during the molting period than the breeding period. Molting sites were associated with early-successional areas for Wood Thrushes (Vega Rivera et al. 1999). Wood Thrush are one of the species experiencing population declines in North America, with more severe declines occurring in the northern parts of their breeding range (Sauer et al. 2011), and thus replication of a study similar to Vega Rivera et al. (1999) is important for conservation of Wood Thrush. Here, we explore whether habitat, physiological condition and/or nest success predicts whether Wood Thrushes breeding at a northern site in Pennsylvania stay on-territory or disperse to a different habitat during breeding and molt.

METHODS

Study Site and Species.—We studied a population of Wood Thrushes (*Hylocichla mustelina*) at the Hemlock Hill Biological Research Area in Crawford County, Pennsylvania, USA (41° 46′ N, 79° 56′ W), for two breeding seasons (25 Apr to 20 Sep 2007–2008), and used radio-telemetry to monitor off-territory movements and molting locations. Our study area supported ~ 60 breeding pairs of Wood Thrushes annually and was a 120-ha subsection of 180-ha mixed hardwood forest, dominated by sugar maples (*Acer saccharum*), American beech (*Fagus grandifolia*), and eastern hemlock (*Tsuga canadensis*). The forest has experienced several logging events that created heterogenous age structure with old (~80 yrs), mid (~40 yrs), and young (<20 yrs) areas, with Wood Thrush nesting throughout.

Capture.—We attempted to capture all pairs at least once during the breeding season using a combination of active and passive mist netting near nest sites. All individuals were banded with USFWS aluminum bands and color banded with unique color combinations and sexed by the presence of a brood patch (Pyle et al. 1997). Wood Thrushes were aged as either 1-year olds (second year, SY) or ≥2-year olds (after second year, ASY) by the amount of primary covert wear as based on Pyle et al. (1997).

In 2007, nine female Wood Thrushes were recaptured in July, and radio-tags (<5% of mass;

1.5 g BD-2 10–14 week battery, Holohil Systems Inc., Carp, Ontario, Canada) were attached using a figure-eight harness of polypropylene thread looped through pre-manufactured holes in the transmitter (Rappole and Tipton 1991). In 2008, we put radio-tags on 23 female and 16 male Wood Thrushes early in the breeding season to better monitor nesting and for capture of molting Wood Thrushes. We used R-1000 (Communications Specialists Inc., Orange, California, USA) receivers and Yagi 3-element antennae to track Wood Thrushes. In another study, the attachment of radio-tags on Wood Thrushes did not negatively impact their breeding behavior or physiological condition during breeding or molt (Gow et al. 2011).

Nesting Activity and Monitoring.—Nests of Wood Thrushes were found during all stages by manually searching territories daily or using radio-telemetry 4–10 days after nest failure. We spent 10–25 person hours/day nest searching. Nest searching effort did not differ per year, except for the use of more extensive radio-telemetry to find subsequent nests in 2008.

Territories were mapped for every pair on a daily basis by recording the locations of singing males and interactions between two males that indicated a territory boundary. Territories of Wood Thrushes ranged in size from ~50–150 m^2, with most in the 50–100 m^2 range, but territory boundaries were not stable throughout the breeding season often shifting no more than 50 m in one direction, and commonly occurred after successful fledgling of the nest. We considered birds to have moved off-territory if they nested >200 m from their previous nesting attempt. We used this 200-m cut-off because territories of Wood Thrushes were typically <150 m across. We used the same cut-off of 200 m for our analysis during molt.

Nest heights ranged from 0.5 m to over 30 m, and we could only closely monitor nests that were ≤15 m. Nests >2 m high were monitored visually or using a pole with a mirror attached to determine presence of first egg, hatch date, and nest failure. Nests were checked visually for failure every day. Nests were considered to have fledged if the nest was empty 12 days after hatching, and we confirmed fledgling by searching for fledglings in the vicinity of nests. Nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) was minimal because of the active removal of female cowbirds for other studies being conducted on the study site, but we observed a total of four nests that were destroyed by cowbirds that either punctured eggs or killed nestlings. The most common source of nest failure was nest predation and common potential predators at the study site included eastern chipmunks (*Tamias striatus*), American Crows (*Corvus brachyrhynchos*), Blue Jays (*Cyanocitta cristata*), Barred Owls (*Strix varia*), black rat snakes (*Elaphe obsoleta*) and ermine (*Mustela erminea*).

Reproductive Success.—We tested the hypothesis that investment in the previous nest influenced if a female moved off-territory to re-nest using a binomial general linear model (GLM). Our model consisted of only first nesting attempts; the response variable was whether a female stayed on-territory or moved off-territory for her next nesting attempt, and predictor variables were clutch size, nest fate (success or failure), female age (SY or ASY), and the interaction effects of female age*clutch size, and female age*nest fate. We used Wilcoxon rank sum tests to examine the consequences of moving off-territory (predictor) on fledging success, nest success, and clutch size (response variables).

Habitat.—We reduced the dimensionality of the habitat variables using non-metric dimensional scaling (NMDS) and then conducted subsequent analyses with the NMDS scores to test the hypothesis that the structural characteristics of the nest site or territory habitat changed between nesting attempts if females dispersed off-territory. NMDS uses an iterative approach and ranks distance instead of using absolute distances; therefore, it has several advantages over other unconstrained ordination methods because data can be non-normal (including zero-truncated data), discontinuous, or non-linear, and thus it is commonly used in community ecology and habitat analyses (McCune and Grace 2002, Zuur et al. 2007).

We measured nest vegetation in a single 10 × 10 m quadrat with the nest as the center of the quadrat. We recorded species and diameter at breast height (DBH) of trees with DBH >7.6 cm and assigned them to two categories: small ≤30 cm, and large ≥31 cm. Wood Thrushes frequently nest low to the ground and forage on the ground (Evans et al. 2011), and measures of ground concealment may be important habitat variables for them. Therefore, we counted the number of shrubs (woody stems with DBH ≤ 7.5 cm) in two categories: ≤60 cm and ≥61 cm. We also estimated the percent leaf litter to the

nearest 10% and measured percent ground cover using a 4.5-cm diameter tube held at waist height along the quadrat axis for 20 spots and indicated the presence or absence of green ground cover. We measured percent canopy cover with a forestry concave densitometer and maximum canopy and nest height with a clinometer.

Our data consist of count data and percent cover. We standardized each variable within a range of 0–1, which retains the position of each value with respect to other values. The structure of the nest vegetation data (n = 86 nests) was uneven with some variables being normally distributed and others slightly skewed with a large number of zeros, or low abundances driving the skew. In multivariate ordination analyses, a matrix of distances or dissimilarities is first constructed and NMDS has an advantage that it uses any distance measure or transformation (McCune and Grace 2002). We used the Bray-Curtis dissimilarity metric, because it is considered robust for datasets similar to ours (i.e., lots of zeros) and is the most common distance metric used in ecology (Faith et al. 1987). In brief, it sums the absolute distance between each count and then divides the sum of the abundances in the two samples followed by a scaling of the values between 0–1 (McCune and Grace 2002).

In NMDS, stress is used to discriminate the appropriate dimensionality of the ordination, and the appropriate dimensionality can be determined by first calculating stress for different numbers of axes, and then created a scree plot to determine stress as a function of the dimensionality (McCune and Grace 2002, Zuur et al. 2007). We additionally used Procrustes plots to visually assess differences in the locations of points between dimensions (McCune and Grace 2002, Oksanen et al. 2012). Similar to other ordination methods, component scores (NMDS scores) are produced and indicate the position of each point in the multidimensional habitat space and can be used as a variable representing the habitat variables ordinated to that axis in future analysis. The NMDS analysis was conducted using package vegan in R 2.14.2 (Oksanen et al. 2012, R Development Core Team 2012).

We used a matched pairs t-test in JMP 8.0.2 (SAS Institute 2009) to determine if females changed nesting site habitats (i.e., NMDS1, NMDS2, and NMDS3 scores), from first to second nests for nesting attempts where the female stayed on-territory versus those that moved off-territory. Next, we tested if the change in habitat between first and second nests was due to a time of season effect and used a linear mixed effects model (lme) with the response variable of first egg date, and predictor variables of each NMDS axes; to account for repeated measures, we included individual as a random factor. We compared original territory habitat (NMDS scores) between females that moved off-territory and those that stayed by using t-tests to determine if territory habitat influenced the number of eggs laid or the number of young fledged (e.g., nest success) of first nests.

Physiological Condition.—To determine if food limitation (i.e., a reduced nutritional state) on a territory influenced whether a female stayed on-territory or moved off-territory for her subsequent nest, we assessed baseline and stress-induced corticosterone (CORT) levels and plasma lipid metabolites of 21 female Wood Thrushes during their first and second nesting attempts, by setting up several (2–5) mist-nets close to their nests. All nets were closely monitored and blood samples were taken within 3 mins from the moment of capture, and provided baseline CORT samples. We followed the same procedures as Done et al. (2011) for blood sampling and the CORT and plasma metabolite assays.

We tested the hypothesis that nutritional state during the first nesting attempt would dictate whether a female moved off-territory for a subsequent nest, by using plasma lipid metabolites TRIG, BUTY, and GLYC, and the physiological condition measures of baseline CORT. For nests with repeat sampling (both incubation and nestling), we used the last sample prior to nest failure or success. TRIG, BUTY, GLYC and CORT were not found to differ significantly between the nesting and incubation periods (Done et al. 2011). We used a binomial GLM to test if females that were nutritionally stressed were more likely to move off-territory between nesting attempts. Our model consisted of a binomial response variable of nesting on- or off- territory for the subsequent nest, and predictor variables of CORT, BUTY, GLYC and TRIG. If females were sampled twice at different nesting attempts, only one of their nesting attempts was used in the analysis, as determined by a coin toss (n = 2).

Molt

During the molting period following breeding, Wood Thrushes became very secretive, quiet, and

TABLE 1. The number of females that re-nested on- versus off-territory (>200 m) following unsuccessful versus successful first nests. Results reported separately for females with radio-tags and females without radio-tags. The unknown category includes birds that were not observed on the study site again.

	Unsuccessful			Successful			Total		
	On	Off	Unknown	On	Off	Unknown	On	Off	Unknown
No tag	6	0	15	6	0	0	12	0	15
Tagged	8	4	0	8	3	0	16	7	0

difficult to locate. The capture rate was low (~ 0.006 Wood Thrush/net hour) using passive mist netting (30–50 nets), and we caught three birds of known breeding history with this method. Using 4–7 people, we caught 25/33 radio-tagged individuals remaining on our study site by slowly flushing/corralling each bird towards a line of mist nets. The other radio-tagged birds remained high in the canopy and thus could not be caught in the ground-level mist nets.

Age, Sex, and Relative Molt.—We tested whether males or females or age differences influenced whether an individual molted off-territory or on-territory using a binomial GLM. Our GLM consisted of a response variable of molting on- or off-territory, and predictor variables of sex, age (SY vs. ASY), and their interaction effect. We tested if birds that started molt earlier molted off-territory by quantifying the extent of flight feather molt. We assigned each of the nine primaries, six secondaries, three tertials and six rectrices on the left side a score between 0–5 based on its stage of growth and used the same protocol and methods as Stutchbury et al. (2011).

Habitat and Molt Dispersal.—We compared the molting habitat of Wood Thrushes to nesting habitat by using NMDS with territory habitat and molting habitat and measuring the same variables as for the nest sites, minus nest height. We measured molt habitat vegetation with 17 quadrats at molting sites for Wood Thrushes. To measure territory vegetation, we adapted the methods of James and Shugart (1970) and used four 10 × 10 m square quadrats per territory; locations were first randomized by determining the center of the territory and the other three quadrats radiating from the center 20 m at 120°, 240° and 360°. Because each territory of vegetation consisted of four separate quadrats, while each molting location consisted of only one quadrat, we standardized the data by averaging the territory plots (total territory vegetation/number of plots). We used the Bray-Curtis distance metric and a range standardization. We then used *t*-tests with the NMDS scores to compare molting versus territory habitat.

All statistical analyses were conducted using R 2.14.2 (R Development Core Team 2012) unless otherwise noted. For our lme models, we checked for normality and homogeneity by visually inspecting plots of the residuals against the fitted values. To assess the validity of our mixed effects models, we used likelihood ratio tests that compared the models with fixed effects to a null model with only random effects (Zuur et al. 2009). All of our models with fixed effects differed from our null models significantly; therefore, we did not reject any of our models. For the linear mixed-effects models we used the lmer function in the lme4 package (Bates et al. 2011) and obtained *P*-values using the pvals.fnc function in the languageR package (Baayen 2011). All statistical tests were two-tailed and variance was expressed as the mean ± SE, and significance set to $P \leq 0.05$).

RESULTS

In 2007, when radio-telemetry was not used to help locate nests, no off-territory dispersal was documented. Only six females had successful first nests and stayed on-territory, while 21 females were unsuccessful, with six remaining on-territory to re-nest. The remaining 15 unsuccessful females were not seen again, despite intensive nest searching on the original and neighboring territories (Table 1).

In 2008, radio-telemetry was used to determine the dispersal decisions of females ($n = 23$). One third (4/12) of females with unsuccessful first nests re-nested off-territory (250–628 m away, mean = 418 m), including one female that left the study site and was not detected again, while 27% (3/11) of females with successful first nests moved off-territory for their second brood (250–558 m away, mean = 381 m; Table 1). All

radio-tagged females with unsuccessful first nests re-mated with the same mate, including those that shifted territories. Of the three females with a successful nest that moved off-territory, two re-mated with their original mate, and one re-nested with a different mate, while her former mate remained unmated on the original territory.

Nest Site Habitat and Dispersal.—We used a multivariate approach (NMDS) to test if females who moved off-territory between nesting attempts changed their nest site habitat. In our NMDS of nesting habitat we retained three axes and had a stress value of 13.6, and an adjusted r^2 fit of 0.88, which is good for ecological data (McCune and Grace 2002, Zuur et al. 2007). Large NMDS1 scores were associated with nest sites with few large trees, a short max canopy, a high percent ground cover and percent canopy cover. Individuals with high NMDS2 values were those occupying nest sites with few shrubs (<60 cm and <60 cm), a low percent leaf litter, and a high nest height. While individuals with high NMDS3 scores had nest sites with few small trees (Fig. 1).

Birds that dispersed off-territory occupied first nests with lots of trees, high canopy height, and a low percent canopy cover and ground cover (NMDS1: $t = -5.06$, df = 30, $P < 0.0001$; Fig. 1a). The number of shrubs, leaf litter, nest height, and the number of small trees did not significantly differ in birds that moved off-territory (NMDS2: $t = -0.55$, df = 14, $P = 0.59$; NMDS3: $t = -0.68$, df = 14, $P = 0.51$). Following dispersal, the nesting sites of birds that moved versus stayed were not significantly different in any habitat variables (NMDS1: $t = -0.096$, df = 15, $P = 0.93$; NMDS2: $t = 0.4$, df = 15, $P = 0.7$; NMDS3: $t = 0.09$, df = 15, $P = 0.93$; Fig. 1b).

Because there was a significant difference in nesting habitat between females that stayed versus those that left, we wanted to see if this change was caused by an overall shift in nesting habitat by all females. We used a matched pairs *t*-test to assess if habitat changed between first and second nests for individual females. There were significant movements to nest sites with few large trees, short canopy height, high percent canopy and ground cover (i.e., higher NMDS1 scores) for birds that moved off-territory, but also for birds that remained on-territory, but no differences in other habitat variables (i.e., NMDS2 or NMDS3 scores) for birds that stayed versus those that moved off-territory (Table 2).

Nutritional Condition and Nesting Dispersal.—We tested the prediction that females who moved off-territory would be of a poorer nutritional state prior to dispersal by using a binomial GLM. Contrary to our prediction, female Wood Thrushes that left their territory may have been of a better nutritional condition, with lower BUTY levels, than those that stayed on-territory for their next nest ($Z = 1.97$, df = 2, 20, $P = 0.048$; means: on = 0.43 ± 0.05, off = 0.28 ± 0.027). There were no significant differences in the levels of GLYC ($Z = 0.27$, df = 2, 20, $P = 0.78$; means: on = 0.37 ± 0.05, off = 0.34 ± 0.08), TRIG ($Z = -1.04$, df = 2, 20, $P = 0.3$; means: on = 1.37 ± 0.14, off = 1.59 ± 0.32), and CORT ($Z = -0.32$, df = 2, 20, $P = 0.75$; means: on = 6.62 ± 2.0, off = 5.35 ± 1.26) for birds that left their territory versus those that stayed.

Reproductive Success.—We tested if moving off-territory to re-nest was predicted by female age, nest success of the first nest or clutch size. In the GLM we removed the interaction effects because they were not significant. There were no significant age ($Z = 0.38$, df = 2, 34, $P = 0.7$), clutch size ($Z = -1.4$, df = 2, 34, $P = 0.16$) or nest fate effects ($Z = 1.04$, df = 2, 34, $P = 0.16$; Table 3) on within-season dispersal. In addition, we looked at the consequences of moving off-territory. The number of young fledged and nesting success were highly correlated ($r = 0.84$, $P < 0.0001$, $n = 30$) so we only analyzed the number of young fledged. Birds that moved off-territory did not increase their clutch size ($Z = -0.15$, df = 25, $P = 0.88$), or fledge more young ($Z = -1.34$, df = 25, $P = 0.18$) than those that stayed on-territory (Table 3). Based on a lme of first egg date against nest habitat, later nests had more ground cover, short canopy and few large trees (NMDS1: $t = 2.15$, df = 69, 34, $P = 0.035$), while there was no significant difference in other habitat variables (NMDS2: $t = -0.76$, df = 69, 34, $P = 0.45$; NMDS3: $t_{69,34} = 0.38$, df = 69, 34, $P = 0.71$).

Molt Dispersal.—In 2007, 4 of 9 birds (44%) radio-tagged during late nesting dispersed off the study site during molt in August, and in 2008, 9/37 (24%) of radio-tagged birds dispersed >1 km away from the study site (i.e., out of radio-telemetry range). None of these birds were relocated despite our search for signals in adjacent woodlots. For both years combined, 18/46 birds (39%) molted on their breeding territory within the study site, 15/46 (33%) molted off-territory

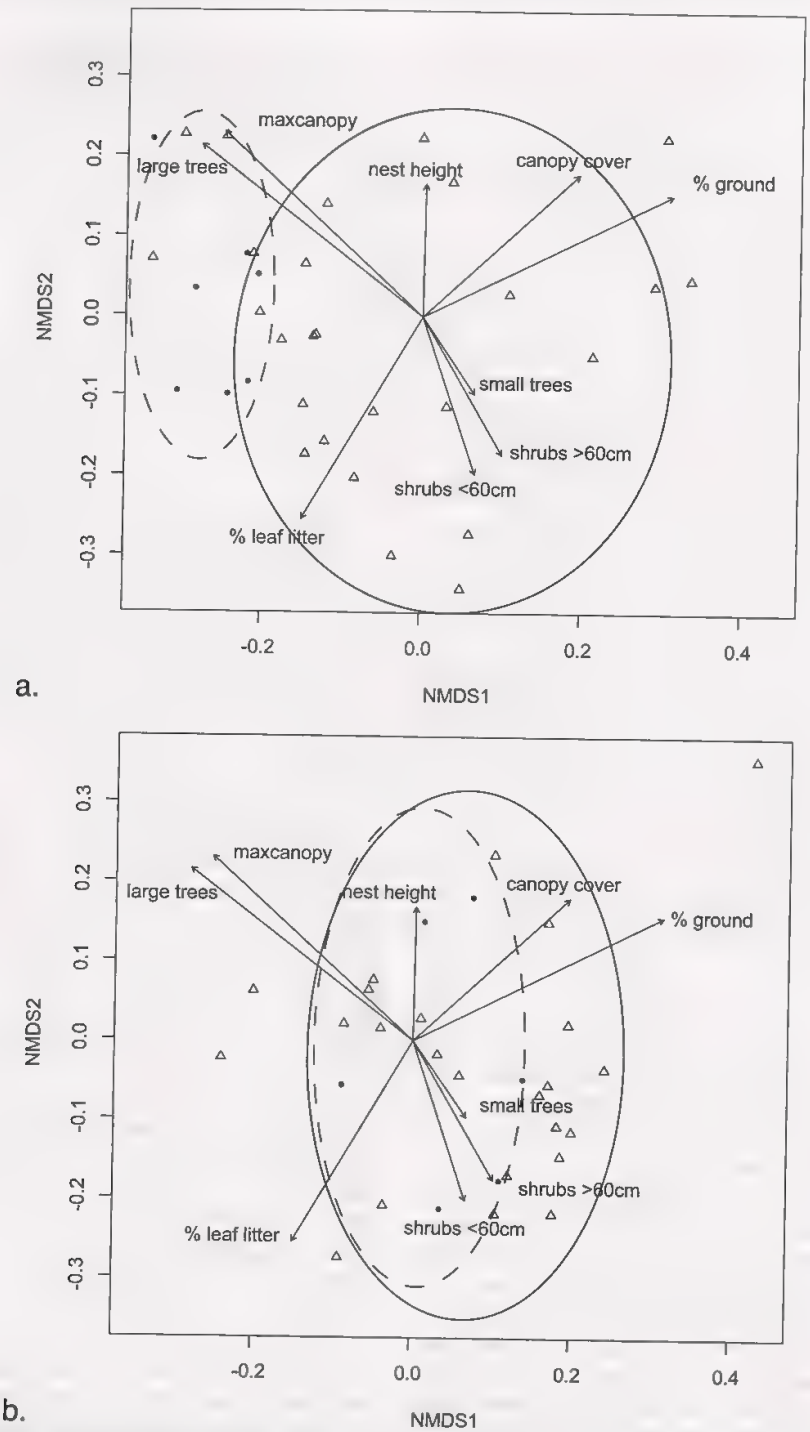

FIG. 1. An NMDS ordination triplot, using the Bray-Curtis distance metric, of nest site habitat for birds that stayed on-territory (solid lines) or moved off-territory (dashed lines) following their first nesting attempt. Each point represents off-territory (filled dots) and on-territory (open triangles) nests in vegetation space. The vectors represent the habitat variables. (a) represents the location of each nest in habitat space for first nests (n = 38), while (b) represents the location of second nests in habitat space (n = 31). The length of the vectors indicate the strength of the variable (i.e., weak predictors have short arrows, strong predictors have long arrows). The angle of the vectors indicate which axis it is most strongly affecting, and the direction indicates whether it is a positive or negative relationship. The ellipses show the clustering of nests between off-territory nests (dashed) and on-territory nests (solid).

TABLE 2. Results from matched pairs *t*-tests examining if female exhibited an overall shift in nest site habitat for females that stayed on-territory after their first nest and those that moved off-territory. Means are expressed as ± SE, $n_{on} = 7$, $n_{off} = 26$.

	Off					On				
Axis	*t*	df	*P*	Mean nest1	Mean nest2	*t*	df	*P*	Mean nest1	Mean nest2
NMDS1	6.23	6	0.0008[a]	−0.26 ± 0.019	0.071 ± 0.038	2.40	25	0.024[a]	−0.046 ± 0.036	0.067 ± 0.031
NMDS2	−0.89	6	0.41	0.062 ± 0.04	0.073 ± 0.059	−0.1	25	0.92	0.016 ± 0.032	−0.044 ± 0.028
NMDS3	−2.26	6	0.064	0.061 ± 0.031	0.028 ± 0.045	−1.76	25	0.091	0.045 ± 0.024	−0.038 ± 0.023

[a] $P \leq 0.05$

within the study site (four of which were still breeding), and 13/46 (28%) birds moved off the study site during the molt period (Fig. 2), and two died prior to molt.

In our NMDS of nesting habitat and molt habitat, we retained two axes and had a stress value of 18 and an adjusted r^2 fit of 0.90. Positive NMDS1 scores are indicative of a high percent canopy cover, few shrubs <60 cm, few shrubs >60 cm, and few fruiting trees. Positive NMDS2 scores are indicative of a low max canopy, low percent ground cover, high leaf litter, few small trees, and few large trees (Fig. 3). Molting habitat differed significantly from nesting habitat by having a low percent canopy cover, more shrubs <60 cm, and >60 cm, and more fruiting trees (NMDS1: $t = 3.41$, df = 20, $P = 0.0028$, NMDS2: $t = -1.65$, df = 20, $P = 0.11$; Fig. 3).

Age and Sex Differences.—We tested the prediction that males and older birds would be more likely to molt off-territory using a binomial GLM based on all radio-tagged birds ($n = 46$). Females were more likely to molt off-territory (20 of 29; 69%) than males (8 of 17; 47%), but the difference was not significant ($Z = -1.11$, df = 25, $P = 0.27$). First-year breeders also tended to molt off-territory (18 of 21; 86%) compared with older birds (14 of 27; 52%; $Z = -1.15$, df = 25, $P = 0.25$; $on_{asy} = 13$, $off_{asy} = 14$; $on_{sy} = 3$, $off_{sy} = 18$), and there was no interaction effect between age and sex ($Z = 0.73$, df = 25, $P = 0.47$). There was no difference in relative molt scores (i.e., whether individuals are relatively advanced versus delayed in stage of molt) between birds molting on-territory versus those that molted off-territory ($t = -0.81$, df = 14, $P = 0.43$). Late breeding individuals were also not more likely to move off-territory to molt ($t = 0.53$, df = 29, $P = 0.6$).

DISCUSSION

We have demonstrated using radio-telemetry that 30% of females dispersed to different territories within the breeding season. We did not find strong support for either the food limitation hypothesis or the predation avoidance hypothesis; however, our data support the hypothesis that females disperse to upgrade their habitat. Nest habitat was significantly different between original and new territories but there was also an overall nest habitat shift for birds renesting within the same territory. One potential reason is that the habitat shift could be due to time of season effects. We found later nests were

TABLE 3. The average clutch size, percentage of ASY (after-second year) females, number of young fledged, and percent of successful nests for first nests and second nest in relation to whether a female stayed on-territory for her subsequent nest or moved off-territory.

	First nests (prior to move)		Second nests (after move)	
Variable	Stayed on-territory	Subsequently dispersed	On-territory	Off-territory
Clutch size	3.0 ± 0.25	3.5 ± 0.34	2.7 ± 0.22	2.67 ± 0.33
Age class (% ASY)	36.7	43.6	NA	NA
No. fledged	1.59 ± 0.34	1.33 ± 0.71	0.7 ± 0.26	0
% successful	40	43	20	0
Sample size	32	7	30	6

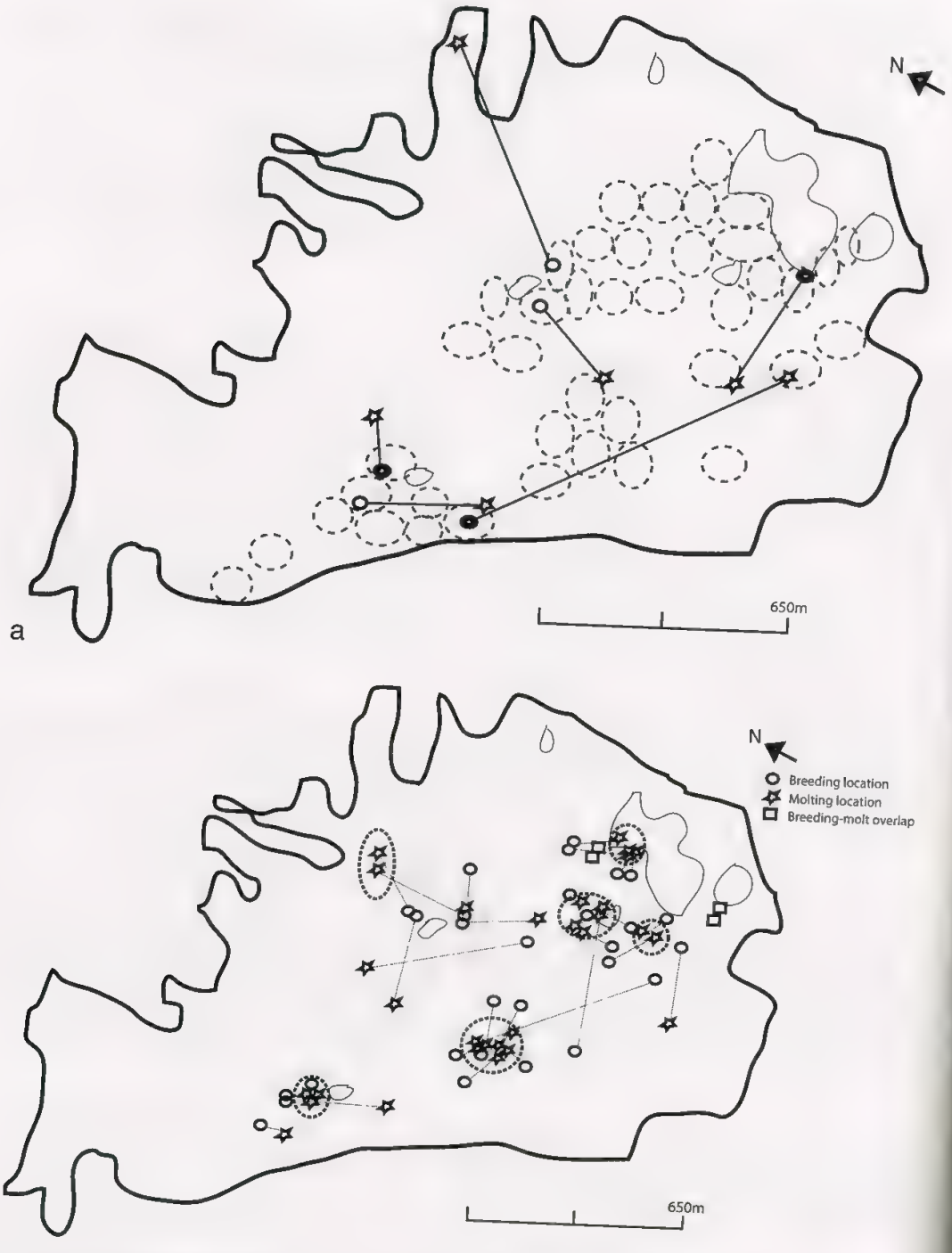

FIG. 2. Maps of the study site showing: (a) the locations of breeding territories in 2008 (all birds monitored during breeding), and off-territory movements of 6 Wood Thrushes (one moved off study site). The stars indicate the location the female moved to, and the closed circles indicate successful first nests, and the open circles unsuccessful first nests; (b) The movements from breeding sites (dots) to molting sites (stars) from Wood Thrushes (n = 31) with known breeding and molt locations (2007 and 2008). The shaded circles indicate open clearings in the forest, and the dashed lines indicate territory boundaries in (a) and concentrations of molting birds in (b).

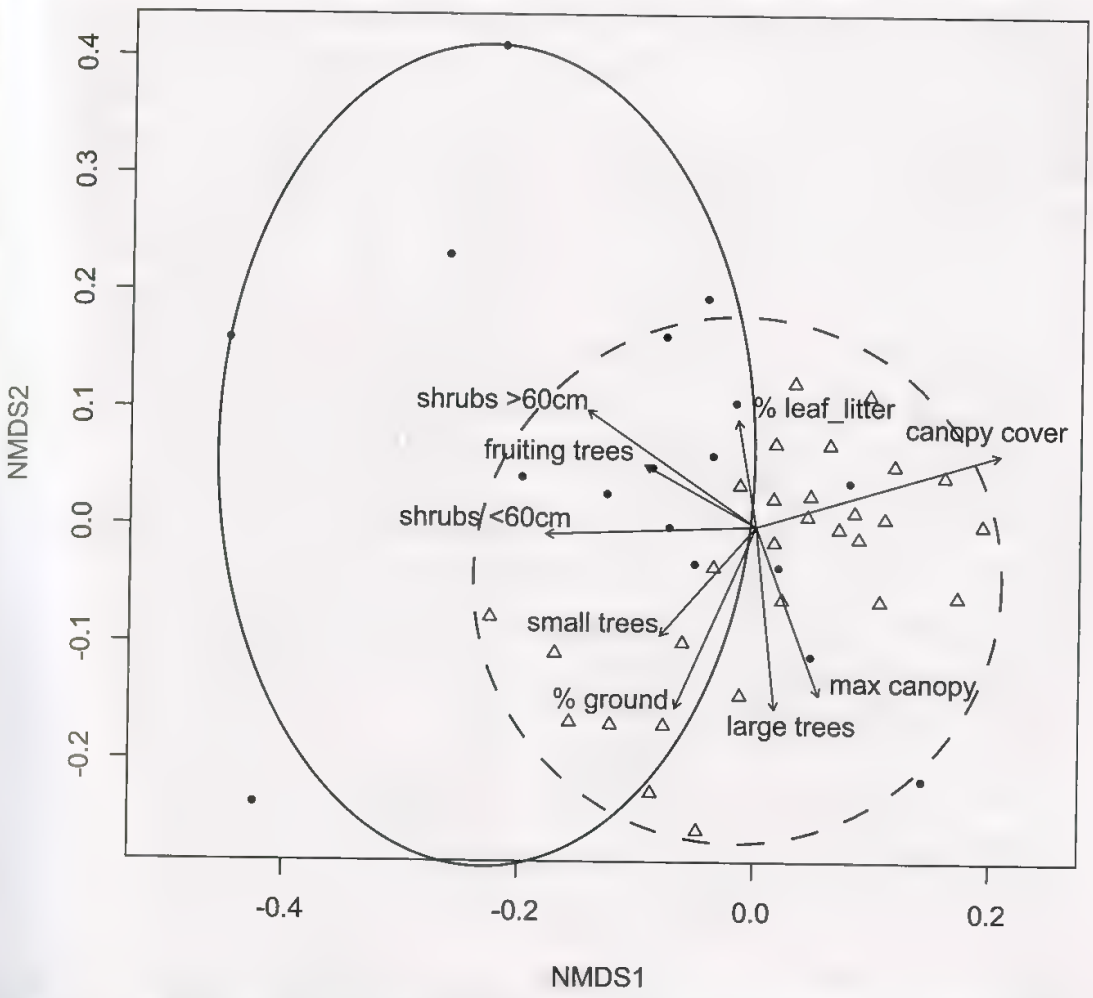

FIG. 3. An NMDS triplot, of molting habitat (solid lines) and territory habitat (dashed lines). Each point represents molting habitat (filled dots) and territory (open triangles) in vegetation space. The vectors represent the habitat variables. The length of the vector indicates the strength of the variable, (i.e., weak predictors have short arrows, strong predictors have long arrows). The angle of the vectors indicate which axis it is most strongly affecting and the direction indicates whether it is a positive or negative relationship.

located in areas with a short canopy height, few large trees, more ground cover, and a higher percent canopy cover; however, these characteristics were opposite to the shift in nesting habitat we observed between first and second nests and thus suggest the habitat shift was not due to a time of season effect. Wood Thrushes may move off-territory to find more preferred nesting habitat that may not be present on their current territory. When birds first arrive on the breeding grounds in spring, some of the cues related to nest site vegetation may not be present (Betts et al. 2008). Birds may shift to higher quality nest sites when opportunities arise such as between breeding seasons (e.g., Calabuig et al. 2008), or potentially within a breeding season (Betts et al. 2008). However, we did not find that nest site habitat predicted nest success of either first or second nests (see also Hoover and Brittingham 1998, Newell and Kostalos 2007), and territory habitat did not predict success of first nests, so it remains unclear how females benefited from shifting territories.

Nest predation may be related to landscape characteristics and predator abundances (Tewksbury et al. 1998, Powell and Frasch 2000) such

that shifting territories could change the probability of nest predation. However, we found that Wood Thrushes with failed nests were not more likely to move off-territory to re-nest, but reasons why some females may disperse off-territory for subsequent nests may be species and life history specific. For instance, in Red-winged Blackbirds (*Agelaius phoeniceus*), nest success was not a strong predictor of dispersal distance, and movement may be related to social constraints (Beletsky and Orians 1991). In contrast, Howlett and Stutchbury (1997) found that Hooded Warblers (*Setophaga citrina*) with successful nests moved farther between nesting attempts following successful nests, but not necessary off-territory, and may be because of female avoidance of first brood parental care when initiating her second brood. Orange-breasted Sunbirds (*Anthobaphes violacea*) moved farther after unsuccessful nesting attempts to avoid predation (Grégoire and Cherry 2007). Powell and Frasch (2000) found evidence that females that disperse outside a predator's range would have increased nest success, and predator characteristics may explain the variation in female dispersal between nests. One possible explanation why we did not find support for the predation hypothesis is that females may have innate preferences for specific nest sites, but because of extremely high rates of nest predation at our sites and other fragmented sites (e.g., Donovan et al. 1995) it may be impossible for Wood Thrushes to avoid predation even by moving to new territories.

We did not find support for the food limitation hypothesis. Females with lower BUTY, indicating that glucose levels were high (Jenni-Eiermann and Jenni 1994), during their first nesting attempt were more likely to move off-territory. However, if dispersal was strongly related to a higher energetic-dietary condition then we would additionally expect to see higher levels of TRIG, indicating fat deposition (Jenni-Eiermann and Jenni 1994). Territory selection has been shown to be highly influenced by prey biomass (Burke and Nol 1998) and can increase annual fecundity (Nagy and Holmes 2004). Our study looked at the physiological measures that identified how a bird was coping with its environment, which overall provides a stronger assessment of the energetic and nutritional state of a bird (Guglielmo et al. 2002). However, our sample sizes were low, so we cannot fully confirm that territory resource abundance did not influence dispersal decisions.

One of the challenges with studying dispersal is the expense of using radio-tags and time required to closely monitor females. In our study, we only observed seven birds that dispersed off-territory, so the power of our ability to test our hypotheses on nesting dispersal was low. We suggest, based on post-hoc power analyses, that future studies may need to have upwards of 20 birds in the dispersed off-territory category to effectively test food limitation and nest predation hypotheses. In our study, because 30% of birds dispersed off-territory following first nest failure, ~85–90 females would need to be radio-tagged to conduct statistical tests with enough power to detect significant effects. However, our analysis of habitat differences (power = 0.95), sex effects (power = 0.93), and age effects (power = 0.99) on dispersal movements during molt had appropriate sample sizes to be powerful enough to detect significant differences.

Molting habitat requirements have been found to differ from breeding habitat requirements (Vega Rivera et al. 1999, 2003), and molting Wood Thrushes prefer dense habitat because this habitat contains more predator avoidance areas (Vega Rivera et al. 1999). Sixty-one percent of Wood Thrushes in our study moved off-territory to molt; several individuals completely left the study site. This degree of molt dispersal was found in a previous study where approximately half of molting Wood Thrushes moved up to 11 km from the breeding territory to molt (Vega Rivera et al. 1999). Additionally, 50% of molting Scarlet Tanagers, molted off of their breeding territory, but several birds frequently returned to their breeding territory throughout the molting period (Vega Rivera et al. 2003). Molting Wood Thrushes in our study molted in areas with lots of shrubs and low percent canopy cover in comparison to territory habitat; this finding suggests that early-mid successional habitat is extremely important for Wood Thrushes during molt. Dense habitats were also important for juvenile survival and act as 'safe havens' for birds (Anders et al. 1997, 1998). Contrary to our study, Vega Rivera et al. (1999) did not find that the presence of fruiting trees was common at molting sites for Wood Thrushes. At our study site, black cherry trees (*Prunus serotina*) were common at molting locations and thus provided an important food source for Wood Thrushes, a seasonally frugivorous species (Vitz and Rodewald 2007).

Our study has shown that without the use of radio-telemetry, off-territory movements during the nesting period are difficult to identify. Without radio-telemetry, annual fecundity would be underestimated, because about one third of females switched territories and, even though banded, their re-nests would have gone undetected. Some females re-nested up to 7–8 times, and not all nesting attempts occurred on the same territory. Territory switching occurs in other forest birds as well (e.g., Morton et al. 2010), and may be far more common than presently realized. Territory switching by females has important implications for understanding songbird population dynamics particularly in assessing source/sink dynamics of populations (e.g., Donovan et al. 1995). Many studies estimate season-long fecundity using un-banded populations (e.g., Grzybowski and Pease 2005) or by using fecundity per nest and estimating average number of re-nests and double broods (e.g., Donovan et al. 1995); in these situations territory switching cannot be detected. This could underestimate productivity in large forest patches where females have the option of dispersing several hundred meters or kilometers between breeding territories.

In sum, we found Wood Thrush need a variety of habitats while on the breeding grounds and these requirements differ between each life history stage. During breeding, Wood Thrushes nested in a variety of areas with different vegetative characteristics, and based on our multivariate analysis preferred nest sites with lots of trees, low percent ground cover, and high canopy height. During molt, Wood Thrushes require early-mid successional areas that are characterized by lots of shrubs (both tall and short) and an abundance of fruiting trees. We suggest, in our northern population, similarly to the southern population (Vega Rivera et al. 1999), the conservation of Wood Thrushes requires a combination of forest types in close proximity to each other: mature/middle aged forests for reproduction, and early-mid successional areas with an abundance of fruiting trees during molt.

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UNDERSTANDING NEST SUCCESS AND BROOD PARASITISM IN THE ENDANGERED BLACK-CAPPED VIREO: COMPARISONS WITH TWO SYMPATRIC SONGBIRDS

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ABSTRACT.—Nest predation and brood parasitism likely cause declines in many songbird species, yet the rate of these declines varies among species. Simultaneously studying co-occurring species with overlapping territories provides an opportunity to identify differences among the species that may explain differential reproductive success. We monitored nests of three co-occurring songbird species to determine whether the federally endangered Black-capped Vireo (*Vireo atricapilla*) experienced lower reproductive success than Northern Cardinals (*Cardinalis cardinalis*) and White-eyed Vireos (*V. griseus*) on private lands with and without trapping of brood parasites. We assessed if habitat metrics and nesting phenology were associated with nest success and frequency of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) to determine if these characteristics explain poor reproductive success. We monitored 188 nests in shrubland and ecotones with woodlands in central Texas from 2006–2008. We found species-specific differences in nest success and brood parasitism, year effects, and differential impacts of cowbird trapping. Black-capped Vireos nesting in locations without cowbird trapping experienced the lowest daily survival rate of nests (0.86) and period nest survival (0.01), whereas estimates in locations with cowbird trapping were similar to the other species (0.93 for daily and 0.11 for period nest survival). Nest initiation date was important for predicting brood parasitism, showing high probability of brood parasitism in the middle of the breeding season and low probability during the beginning and end of the season. Habitat metrics were not good predictors of nest success or brood parasitism. Management for conservation of Black-capped Vireos focused on vegetation manipulation may not increase reproductive success in the absence of cowbird trapping in some areas of the breeding range, because daily survival rate of nests was associated with cowbird trapping but not habitat metrics. *Received 7 March 2013. Accepted 2 August 2013.*

Key words: brood parasitism, *Cardinalis cardinalis*, edge effect, *Molothrus ater*, nest survival, *Vireo atricapilla*.

Poor reproductive success is likely one of the primary causes of declines in many songbird species (Martin 1992, Peterjohn et al. 1995). Reproductive success is, in part, constrained by nest success and brood parasitism. These constraints can vary spatially, temporally, and among species. Many songbird species have low reproductive success (e.g., Nice 1957, Ricklefs 1969, Campomizzi et al. 2009) and high frequency of brood parasitism (e.g., Rothstein and Cook 2000, Farrell et al. 2010). Comparisons among co-occurring songbirds, with overlapping territories, exposed to similar risks may elucidate if and reasons why one species may experience low reproductive success compared to other species. Understanding the conditions under which these constraints occur can inform the management of affected species.

The Black-capped Vireo (*Vireo atricapilla*) is a species of conservation concern and co-occurs with White-eyed Vireos (*V. griseus*) and Northern Cardinals (*Cardinalis cardinalis*). Low reproductive success led to concerns that the Black-capped Vireo population was declining, and this was a primary factor for listing them as endangered (USFWS 1991). Previous studies have documented low reproductive success (Kostecke et al. 2005, Campomizzi et al. 2009) and high frequency of brood parasitism (Kostecke et al. 2005, Farrell et al. 2010). The majority of published research about Black-capped Vireos comes from public properties, particularly Fort Hood military base, which has intensive conservation programs that include vegetation restoration and removal of brood parasites (Kostecke et al. 2005; Summers et

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al. 2006a, b; Noa et al. 2007). Research has also occurred on other public properties (e.g., Balcones National Wildlife Refuge, Fort Sill military base, Kerr Wildlife Mangement Area, Wichita Mountains National Wildlife Refuge; Fazio et al. 2004, Barr et al. 2008, Zink et al. 2010, Pope et al. 2013). However, little is known about reproductive success throughout most of the breeding range because >90% of their breeding range occurs on private land (Wilkins et al. 2006, Campomizzi et al. 2009, Farrell et al. 2010, Conkling et al. 2012). Private lands have different land uses than public properties and most are not specifically managed for Black-capped Vireos through vegetation manipulation or removal of brood parasites, although there are conservation programs implemented on some private properties (e.g., Texas Parks and Wildlife Department's Landowner Incentive Program, Environmental Defense Fund's application of safe harbor agreements). Thus, knowledge from studies of reproductive success on public properties may not be applicable to private properties. We addressed this knowledge gap by focusing our research on private land with the understanding that Black-capped Vireos may be rare on private lands, limiting analytical options, but that the information would nevertheless be valuable to improve our understanding of their reproductive success on land ownership comprising the majority of their breeding range.

Nest predation is the most common cause of nest failure in many songbird species (Nice 1957, Ricklefs 1969, Martin 1993), including Black-capped Vireos (Stake and Cimprich 2003, Conkling et al. 2012). Rat snakes (*Elaphe* spp.), fire ants (*Solenopsis* spp.), and Brown-headed Cowbirds (*Molothrus ater*) have been identified as primary predators of nests of Black-capped Vireos in central Texas (Stake and Cimprich 2003, Campomizzi et al. 2009, Conkling et al. 2012). In addition to being a brood parasite, Brown-headed Cowbirds are considered nest predators, because they remove host eggs and nestlings, often causing nest failure. Relationships between nest predation and habitat metrics are complex (Lahti 2001, Chalfoun et al. 2002) and can be specific to the system and species studied.

Patterns of habitat use and abundance have been identified for nest predators of Black-capped Vireos. Edges between woodland and non-woodland were preferred by rat snakes (Blouin-Demers and Weatherhead 2001a, b; Sperry 2008) and also provide for increased activity and abundance of fire ants (Tschinkel 1987, Stiles and Jones 1998) and Brown-headed Cowbirds (Brittingham and Temple 1983, Paton 1994, Howell et al. 2007). Additionally, increases in the proportion of woody cover may lead to decreased predation by Brown-headed Cowbirds (Thompson 1994, Goguen and Mathews 2001), rat snakes, and fire ants (Summerlin et al. 1976, Porter et al. 1988, Porter and Savignano 1990, Stein et al. 1990, Stiles and Jones 1998). Lastly, nest predator activity increased as the season progressed for snakes (Sperry et al. 2008, Sperry and Weatherhead 2008), Brown-headed Cowbirds (Burhans and Thompson 1998), and fire ants (Stein et al. 1990).

Brood parasitism reduces reproductive success in some species (Rothstein and Peer 2005), particularly in Black-capped Vireos (Kostecke et al. 2005, Farrell et al. 2010). As with nest predation, relationships between frequency of parasitism and habitat metrics vary among studies and systems (Paton 1994, Gustafson et al. 2002, Sharp and Kus 2006, Howell et al. 2007). Patterns of cowbird occurrence and parasitism frequency have been described. Brown-headed Cowbirds can be more common near edges between woodland and non-woodland (Brittingham and Temple 1983, Paton 1994, Howell et al. 2007) and landscapes with more woody cover can have lower frequency of parasitism (Brittingham and Temple 1983). Areas with little woody cover may function similar to edges for cowbirds. Additionally, parasitism frequency can be low early in the breeding season, gradually increase to a mid-season peak, and then decrease at the end of the season (Briskie et al. 1990, Woodworth 1999, Hoover et al. 2006). However, the timing of cowbird egg-laying might more closely correspond to the nest initiation date of a particular host species, making one host species more susceptible to parasitism than another host species.

Our objective was to study nest success and brood parasitism in the Black-capped Vireo (*Vireo atricapilla*) to improve our understanding of its reproductive success through comparisons with White-eyed Vireos and Northern Cardinals on private lands in central Texas with and without management for cowbirds. We used comparisons with co-occurring songbirds with overlapping territories exposed to similar risks to investigate if and reasons why Black-capped Vireos may experience low reproductive success. All three

species build open-cup nests, are in the order Passeriformes, and are parasitized by Brown-headed Cowbirds. Although many possible factors could influence differential reproductive success among these species, we investigated broad-level characteristics of the habitat that are likely to influence nest success and brood parasitism based on the ecology of nest predators and brood parasites. We hypothesized (1) Black-capped Vireos would have lower reproductive success as a consequence of lower daily survival rate of nests or longer nesting period (from egg-laying to fledging offspring) compared with the other two species, (2) habitat metrics (woody cover, edge density) around nests of Black-capped Vireos at two spatial scales would be associated with lower reproductive success and greater frequency of brood parasitism by Brown-headed Cowbirds compared to the other two species, and (3) nest initiation date and ordinal date of season for Black-capped Vireo would be associated with time periods of the breeding season with higher parasitism frequency and lower daily survival rate of nests, respectively, compared to the other two species.

METHODS

Study Area.—We conducted this study in the Leon River watershed in central Texas. The study area was within the Limestone Cut Plain level IV eco-region in the Cross Timbers level III eco-region, consisting of broad valleys between mesas on Lower Cretaceous limestone (Griffith et al. 2004). Vegetation where we monitored nests consisted of mid-successional stage shrubland similar to nearby areas previously used for research on Black-capped Vireos (Grzybowski et al. 1994, Bailey and Thompson 2007), ecotones between oak-juniper (*Quercus-Juniperus*) woodland and grassland, and adjacent oak-juniper woodland. The most common species of woody vegetation were oaks, juniper, eastern redbud (*Cercis canadensis*), elbow bush (*Forestiera angustifolia*), and Texas ash (*Fraxinus albicans*). We monitored nests on mesa tops and slopes on the sides of mesas. Elevation in the study area ranged from 200–500 m. We visited privately owned properties that experienced similar disturbance and land management practices typical of the study area including ranching, hunting, and agriculture. We detected Black-capped Vireos in 10 locations during initial surveys on 33 properties within a 140,000-ha area. Locations had 36–103-ha patches of vegetation where we searched for nests. We monitored nests at all 10 locations annually unless Black-capped Vireos were not nesting in a location or we no longer could obtain permission to access properties. Cowbird trapping was conducted during each year with 30–40 traps distributed among five of the nest monitoring locations. A contractor replenished food and water in traps once every two days when temperature was <30 °C, daily when ≥ 30 °C, and euthanized cowbirds by cervical dislocation.

Nest Monitoring.—We searched for nests using behavioral cues and systematic searching (Martin and Geupel 1993) from 15 March to 31 July in 2006–2008 for Black-capped Vireos and White-eyed Vireos, and in 2006 and 2007 for Northern Cardinals. We checked active nests every 3–4 days to record nest contents including host eggs, cowbird eggs, number of young, and age of young. We estimated the age of young based on their size, feather development, and behavior (Grzybowski 1995, Hopp et al. 1995). We recorded the date each nest was found and, based on successive checks, either observed when the first host egg was laid in each nest or back-dated nests to estimate nest initiation date for nests found after eggs were laid (Mayfield 1975).

We considered a nest successful if ≥ 1 host young fledged from the nest. We determined fledging by observations of adults carrying food to fledglings or detection of fledglings by sight or sound near nests that had large nestlings near fledging age on our previous nest check. We considered nests failed if they were empty after having eggs or if we did not detect fledglings or observe adults carrying food near nests that previously had nestlings. Nests that were abandoned by adults in the absence of a partial predation event were excluded from our analyses, because we were unable to determine when the nest became inactive; nest abandonment was rare for all three species. We recorded the location of each nest to ~6-m accuracy using a hand-held global positioning system (GPS).

Habitat Metrics.—We used habitat metrics likely to influence daily survival rate and brood parasitism of nests based on the ecology of nest predators and brood parasites. Our metrics of interest were edge density and woody cover within 100-m and 500-m radii from the nest. We used two spatial scales, because the importance of investigating the relationship between predictor variables and daily survival rate of nests at

TABLE 1. Evaluation of logistic exposure models for predicting daily survival rate of nests of Black-capped Vireos (n = 38), Northern Cardinals (n = 97), and White-eyed Vireos (n = 53) monitored from 2006–2008 in central Texas. Interactions are designated with an asterisk and include additive effects of variables in interaction.

Model [a]	K [b]	AIC_c [c]	ΔAIC_c [d]	w_i [e]	−2 log likelihood
species * year	8	709.96	0.00	0.57	−346.87
species * trap	6	711.61	1.65	0.25	−349.74
species	3	713.70	3.73	0.09	−353.83
intercept	1	714.90	4.93	0.05	−356.44
species * woody cover	6	717.97	8.01	0.01	−352.92
species * edge + trap	7	718.27	8.30	0.01	−352.05
species * edge	6	718.88	8.92	0.01	−353.37
species * date	6	719.06	9.09	0.01	−353.46
species * woody cover + trap	7	719.23	9.26	0.01	−352.53
species * date + trap	7	719.83	9.87	0.00	−352.83

[a] Variables were: species = 3 species studied, trap = trapping for Brown-headed Cowbirds, edge density = density of edge in woody vegetation (m/m²) within 500 m of nests, woody cover = proportion of woody vegetation within 500 m of nest, date = ordinal date of season, year = year nest was active.
[b] Number of parameters in each model.
[c] Akaike's Information Criterion corrected for small sample size.
[d] Difference in AIC_c values compared to the best-fit model
[e] Model weights.

multiple spatial scales is clear in the literature (Chalfoun et al. 2002, Stephens et al. 2003). Thus, we chose a 100-m radius because it exhibits characteristics occurring within a Black-capped Vireo's territory, which is typically 1–4 ha in Texas (Grzybowski 1995), and a 500-m radius because it represents a broader spatial context representative of the landscape through which nest predators and brood parasites move.

We used ArcMap™ 9.2 (ESRI®, Redlands, California, USA) to characterize vegetation within a 100-m and a 500-m radius centered at each nest. We used the ISO cluster and maximum likelihood classifier functions in Spatial Analyst to run an unsupervised classification of a 2005 National Agriculture Image Program (NAIP) aerial image with 2-m grain. We reclassified the unsupervised classification into two classes, woody cover and non-woody cover, for our analyses. We used the ArcMap extension Hawth's tools (available at www.spatialecology.com) to calculate the proportion of pixels classified as woody cover within each radius. We defined edge as the boundary between woody and non-woody vegetation classes and calculated edge density (edge m/area m²) at each spatial scale for each nest. We examined multicollinearity among spatial variables using a variance inflation factor >0.2 as a criterion for removal from the modeling process described below (Graham 2003). Woody cover and edge density were correlated between 100-m and 500-m radii (Black-capped Vireo r = 0.755, Northern Cardinal r = 0.625, White-eyed Vireo r = 0.704). Thus, we used data from the 500-m radii for analyzing daily survival rate of nests because it includes a bird's territory and surrounding landscape (i.e., the scale at which management is likely to occur).

Nest Survival.—We defined daily survival rate as the probability a nest would survive one day and period nest survival as the probability a nest would survive the entire nesting period from laying of the first egg to fledging young (estimated mean 30 days for Black-capped Vireos [Grzybowski 1995], 25 days for Northern Cardinals [Halkin and Linville 1999], and 27 days for White-eyed Vireos [Hopp et al. 1995]). We did not estimate length of nesting period using our data, because few nests of Black-capped Vireos survived the duration of the nesting period. We used ordinal date (i.e., from 1 Jan = 1 to 31 Dec = 365 or 366) to standardize date of season.

We used an information-theoretic approach to evaluate 10 *a priori* logistic exposure models (Shaffer 2004) that addressed differential daily survival rate of nests among our three study species (Table 1). We developed statistical models based on our research hypotheses in the introduction. We predicted that daily survival rate would vary among the three species, thus we considered a single-effects model for species-specific survival and models with an interaction to account for species-specific rela-

TABLE 2. Evaluation of logistic regression models for predicting probability of brood parasitism of nests of Black-capped Vireos (n = 38), Northern Cardinals (n = 97), and White-eyed Vireos (n = 53) monitored from 2006–2008 in central Texas. Interactions are designated with an asterisk and include additive effects of variables in interaction.

Model [a]	K [b]	AIC_c [c]	ΔAIC_c [d]	w_i [e]	−2 log likelihood
species * quadratic date + trap	8	106.78	0.00	0.82	−44.89
species * woody cover 500 m + trap	7	112.07	5.29	0.06	−48.64
species * edge 500 m + trap	7	112.92	6.14	0.04	−49.07
species * woody cover 100 m + trap	7	112.92	6.14	0.04	−49.07
species * trap	6	113.33	6.55	0.03	−50.37
species * edge 100 m + trap	7	115.38	8.59	0.01	−50.30
species * edge 100 m	6	150.03	43.25	0.00	−68.73
species * edge 500 m	6	150.49	43.71	0.00	−68.96
species * quadratic date	7	151.31	44.53	0.00	−68.27
species	3	153.76	46.97	0.00	−73.80
species * woody cover 500 m	6	156.20	49.42	0.00	−71.81
species * woody cover 100 m	6	157.45	50.67	0.00	−72.44
intercept	1	195.99	89.20	0.00	−96.98

[a] Variables were: species = 3 species studied, cowbird trap = trapping for Brown-headed Cowbirds, woody cover 100 m = proportion of woody vegetation within 100 m of nest, woody cover 500 m = proportion of woody vegetation within 500 m of nest, edge density 100 m = density of edge in woody vegetation (m/m^2) within 100 m of nests, edge density 500 m = density of edge in woody vegetation (m/m^2) within 500 m of nests, quadratic date = quadratic ordinal date when first host egg laid in nest.
[b] Number of parameters in each model.
[c] Akaike's Information Criterion corrected for small sample size.
[d] Difference in AIC_c values compared to the best-fit model.
[e] Model weights.

tionships with habitat metrics and ordinal date. We included the additive effect of cowbird trapping to models because of the influence it has on the daily survival rate of nests. We included a model with an interactive effect of species and year because daily survival rate often varies among years. Lastly, we included an intercept-only model to compare model fit assuming a constant daily survival rate with models based on our hypotheses.

We used AIC_c model selection (Akaike Information Criterion corrected for small sample size relative to the number of parameters in the model) to assess relative fit among candidate models (Burnham and Anderson 2002b). We considered models with $\Delta AIC_c < 2.0$ to be competitive for the best model (Burnham and Anderson 2002a). We did not examine a goodness-of-fit of the best-fit model because of poor approximation of the sampling distribution when sample sizes are small, such as they are when including continuous covariates in our candidate models (Shaffer and Thompson 2007). We estimated daily survival rate using coefficients from competitive models. We estimated period nest survival by raising estimates of daily survival rate to the power of the number of days in the nesting period for each species to enable inter-specific comparisons of period nest survival. We used program R 2.15 (R Development Core Team 2012) for conducting analyses and producing figures.

Cowbird Parasitism.—We considered a nest parasitized if we found an egg from a Brown-headed Cowbird in the host nest within 3 days of the first egg laid by the host; this timing enables cowbird eggs to hatch before or with host eggs. We used a similar approach to our analysis for nest survival. We evaluated 13 *a priori* logistic regression models that addressed differential brood parasitism among the three species based on our research hypotheses (Table 2). We included a single-effects model for species-specific parasitism and models with an interaction to account for species-specific relationships with habitat metrics and nest initiation date. We included the additive effect of cowbird trapping to models because of the influence it has on parasitism frequency. Lastly, we included the intercept-only model. We analyzed spatial variables at 100- and 500-m radii centered at each nest because we did not detect multicollinearity in this data set. We used the best-fit model to predict probability of brood parasitism.

RESULTS

Nest Survival.—We monitored 188 nests of Black-capped Vireos (n = 38), White-eyed Vireos (n = 53), and Northern Cardinals (n =

97). The best-fit model for daily nest survival was the interactive effect of species and year (Table 1). The interactive effect of species and cowbird trapping was also a competitive model ($\Delta AIC_c = 1.65$; Table 1). Models including the proportion of woody cover, edge density, or ordinal date were not competitive (Table 1). Mean daily survival rate of nests was higher in 2008 for Black-capped and White-eyed vireos compared to 2006 and 2007 (Fig. 1). Mean daily survival rate of nests for Black-capped Vireos in locations without cowbird trapping was lower (0.86) and outside of 95% confidence intervals than estimates for Black-capped Vireos in locations with cowbird trapping and White-eyed Vireos and Northern Cardinals with and without cowbird trapping (Fig. 1). Period nest survival for Black-capped Vireos was higher in locations with cowbird trapping (0.11) than without trapping (0.01). Period nest survival for White-eyed Vireos was also higher in locations with trapping (0.23) compared to locations without trapping (0.07). In contrast, period nest survival of Northern Cardinals was lower in locations with trapping (0.09) than in locations without trapping (0.15).

Cowbird Parasitism.—Parasitism frequency was 72% for Black-capped Vireos, 6% for Northern Cardinals, and 30% for White-eyed Vireos. Observed median nest initiation date for Black-capped Vireos was 20 days later than Northern Cardinals and 15 days later than White-eyed Vireos. The best-fit model was the interactive effect of species with a quadratic effect of nest initiation date and the additive effect of cowbird trapping (Table 2). Models including proportion of woody cover and edge density within 100- and 500-m radii centered at each nest were not competitive (Table 2). The best-fit model predicted probability of parasitism as relatively low during the beginning and end of the breeding season and high during the middle of the breeding season, but with varying magnitudes depending on species and presence of cowbird trapping (Fig. 2). The greatest probability of brood parasitism was ~1.0 for Black-capped Vireos during the middle of the breeding season in locations without cowbird trapping. Similarly, the probability of brood parasitism for White-eyed Vireos was about 0.8 during the middle of the breeding season without cowbird trapping, whereas for Northern Cardinals the probability did not exceed 0.4 (Fig. 2).

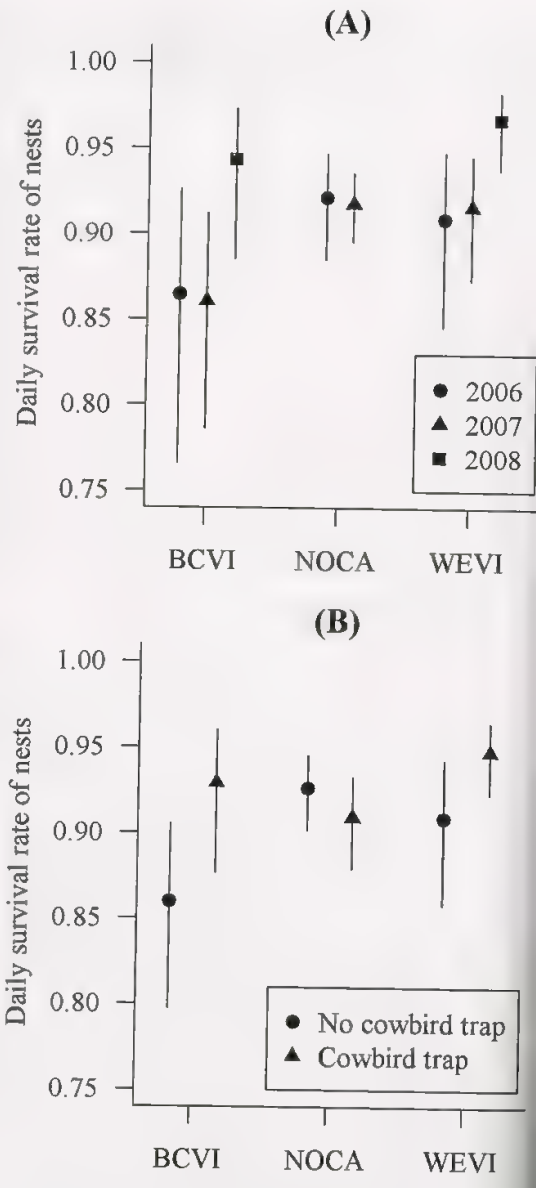

FIG. 1. Predicted daily nest survival rate of Black-capped Vireos (BCVI), Northern Cardinals (NOCA), and White-eyed Vireos (WEVI) based on the two competitive logistic exposure models, the interactive effect of species and year (A) and the interactive effect of species and cowbird trapping (B). We monitored nests ($n = 188$) from 2006–2008 in central Texas (we did not monitor Northern Cardinal nests in 2008). Solid circles, triangles, and squares indicate predicted means and vertical lines indicate 95% confidence intervals.

Cowbird trapping reduced probability of parasitism to near zero for Northern Cardinals, <0.2 for White-eyed Vireos, and <0.5 for Black-capped Vireos (Fig. 2).

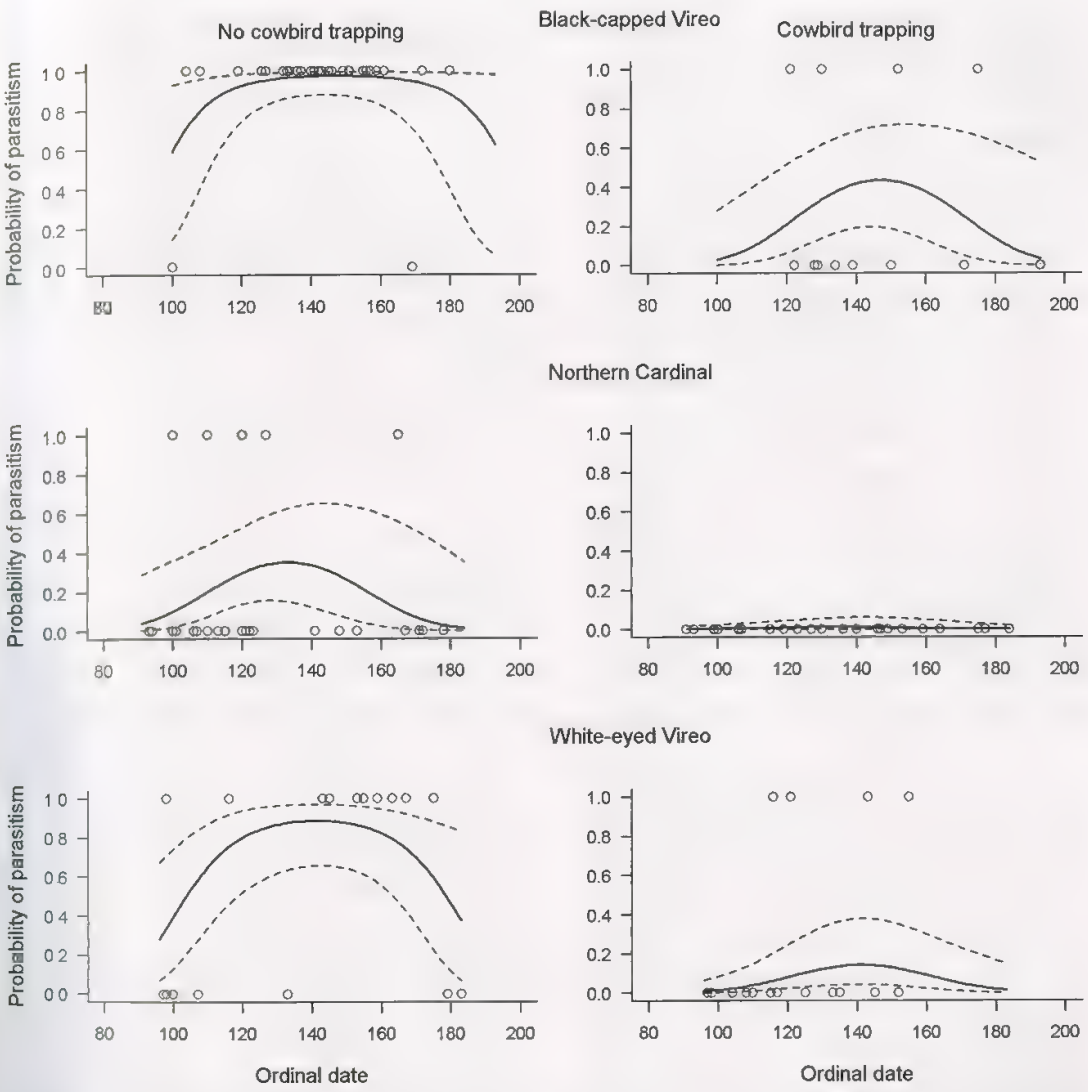

FIG. 2. Predicted probability of nest parasitism by Brown-headed Cowbirds on Black-capped Vireos, Northern Cardinals, and White-eyed Vireos during the range of ordinal nest initiation dates for each species. We used the best-fit logistic regression model (the interactive effect of species and a quadratic effect of nest initiation date and the additive effect of cowbird trapping) to predict probability of parasitism of a nest for each species based on our sample of nests (n = 188) monitored from 2006–2008 in central Texas. Solid lines show predicted means, dashed lines 95% confidence intervals, and open circles observed data.

DISCUSSION

Our study demonstrated species-specific differences in nest success and brood parasitism for three co-occurring songbirds. Additionally, nest success varied among years and removal of Brown-headed Cowbirds through trapping efforts differentially affected species. In locations without cowbird trapping, a combination of low daily survival rate of nests and a long nesting period led to low estimates of period nest survival for Black-capped Vireos compared to the other species. Cowbird trapping increased daily survival rate of nests of Black-capped Vireos to estimates similar to the other species' daily survival rates regardless of cowbird trapping. Without the influence of cowbird trapping, both vireo species experienced high probabilities of brood parasitism; however, the magnitude of the reduction in parasitism from trapping was greater for White-eyed Vireos compared to Black-capped Vireos. Other studies

in patches of habitat of similar size have found similar estimates of daily survival rate for nests of Black-capped Vireos in areas with varying intensity of trapping for cowbirds (Kostecke et al. 2005, Campomizzi et al. 2009).

Contrary to our hypotheses based on the ecology of nest predators, habitat metrics (woody cover, edge density) did not produce competitive models of daily survival rate of nests. Based on previous research on other species, it is possible that particular characteristics of territories and vegetation characteristics at broader spatial extents could be associated with variation in daily survival rate (Thompson et al. 2002) or predator activity (Chalfoun et al. 2002). Similar to our results, previous research for songbirds indicated that reproductive success varies among years (e.g., Morrison and Averill-Murray 2002, Kostecke et al. 2005) and that cowbird trapping can increase reproductive success (Rothstein and Cook 2000). Additionally, the low reproductive success of Black-capped Vireos in our study, particularly in locations without cowbird trapping, could have indirect effects on adult survival (Butler et al. 2008).

Our results indicated Black-capped Vireos were more vulnerable to brood parasitism than the other two co-occurring species because they initiated nests later in the breeding season and possibly other species-specific differences. Although cowbird trapping reduced probability of parasitism for all three species, the probability of parasitism was higher for Black-capped Vireos compared to the other species in locations with and without cowbird trapping. Previous studies have also found relationships between parasitism frequency by Brown-headed Cowbirds and nest initiation date of hosts (Strausberger 1998, Ortega and Ortega 2000, Post van der Burg et al. 2009).

Woody cover and edge density, measured at two spatial scales around nests of Black-capped Vireos, were not associated with greater frequency of brood parasitism compared to the other two species. Previous research found that relationships between frequency of parasitism by Brown-headed Cowbirds and variables based on vegetation and landscape context depend on geographic location (Budnik et al. 2002, Tewksbury et al. 2006, Howell et al. 2007) and host species (Robinson et al. 1995, Burhans 1997, Woolfenden et al. 2003). Barber and Martin (1997) found that measurements of fine-scale nest site characteristics revealed no differences between nests of Black-capped and White-eyed vireos, but vireo nests had less concealment and greater canopy cover than nests of Northern Cardinals; they found no differences in characteristics between parasitized and unparasitized nests for each species. It is also possible that parasitism frequency was associated with landscape variables at larger spatial scales than we included, as was found for songbirds nesting in woodlands (Robinson et al. 1995, Donovan et al. 1997). Such relationships may occur because cowbirds can commute up to 8 km between locations for feeding and parasitizing (Goguen and Mathews 2001, Kostecke et al. 2003).

Future studies could examine relationships between daily survival rate of nests and habitat metrics for Black-capped Vireos at larger spatial scales. Additionally, future research could address factors we were unable to evaluate, such as multiple brooding among the three species which is largely undocumented (Grzybowski 1995, Hopp et al. 1995, Halkin and Linville 1999), but which could influence population level responses to period nest survival. Similarly, population trajectory could vary among the three species because of variation in clutch size: White-eyed Vireos have a larger average clutch size of four (Hopp et al. 1995) compared to Black-capped Vireos, which average 3–4 (Grzybowski 1995), and Northern Cardinals which average 2–3 eggs per clutch (Halkin and Linville 1999).

Our inter-specific comparisons provided insight into why a species of conservation concern may have lower reproductive success than co-occurring species. Our results suggested cowbirds have more of an impact on Black-capped Vireos than Northern Cardinals and White-eyed Vireos where the species co-occur. Our study is unique because we provided nest success and brood parasitism estimates for the endangered Black-capped Vireo relative to two co-occurring species. Nest survival and brood parasitism estimates have limited meaning without comparative estimates, such as trends over time or across geographical locations, or, as in our case, co-occurring species. Furthermore, our study occurred on private properties, many of which did not have active habitat management practices for Black-capped Vireos. As demonstrated by our study, cowbird trapping alters local estimates of reproductive success, suggesting that studies conducted on properties that actively remove cowbirds do not adequately represent conditions occurring on unmanaged

lands. Our results suggest that cowbird removal, in addition to reducing parasitism, may be crucial for increasing period nest survival because it also reduces the nest predator effects of cowbirds.

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NEST SURVIVAL AND BREEDING BIOLOGY OF THE PUERTO RICAN BULLFINCH (*LOXIGILLA PORTORICENSIS*) IN SOUTHWESTERN PUERTO RICO

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ABSTRACT.—Breeding biology information, including nest survival estimates, are lacking for many nesting species in Puerto Rico. We studied the endemic Puerto Rican Bullfinch (*Loxigilla portoricensis*), and modeled daily nest survival to better understand the effects of several factors on daily nest survival. In 2009 and 2010 we monitored 37 bullfinch nests at two sites in southwestern Puerto Rico. Predation was the most important cause of nest failure. Ten nest survival models received approximately equal support. No temporal trends in nest survival were supported over others. Results suggested that available fruit is important for successful nesting, increased precipitation is related to higher nest survival, nest survival varied by site, and increased nest height is related to lower nest survival in bullfinches. Under the top model, daily nest survival rates for each site and nest stage ranged from 0.83–0.86% in 2009 and 0.80–0.93% in 2010. This information on nest survival and factors that influence it increases our understanding of the breeding biology of the bullfinch, and will ultimately help inform future studies and conservation efforts in southwestern Puerto Rico. *Received 8 November 2012. Accepted 29 July 2013.*

Key words: breeding biology, bullfinch, frugivory, *Loxigilla*, nest survival, Puerto Rico.

The endemic Puerto Rican Bullfinch (*Loxigilla portoricensis*), a frugivorous species of the family Emberizidae, is common in forests and brushy areas throughout most of Puerto Rico (Raffaele 1989, García et al. 2005). However, many aspects of its life history are poorly understood, including its breeding biology. Little published literature exists on this subject aside from brief descriptions of nests, nesting habits, and clutch size (Bowdish 1901, 1903; Wetmore 1916; Gleffe et al. 2006), each of which is based on only a few observations.

The genus *Loxigilla* is endemic to the Caribbean and contains three species in addition to the Puerto Rican Bullfinch: the Greater Antillean Bullfinch (*L. violacea*) of the Bahamas, Hispaniola, Jamaica, and Turks and Caicos; the Lesser Antillean Bullfinch (*L. noctis*), inhabiting Lesser Antillean Islands from the Virgin Islands south to Grenada, except for Barbados; and the Barbados Bullfinch (*L. barbadensis*), found only on Barbados. Much like the Puerto Rican Bullfinch, the other three species of bullfinches are poorly studied. All *Loxigilla* species are primarily frugivorous (Wetmore 1916, Danforth 1939, Lack 1976, Adolph and Roughgarden 1983) and consume fruit from a wide variety of native and introduced plant species (Greenlaw 1990). All species are described as constructing domed or globular nests and laying clutches of 2–3 eggs (Bowdish 1903, Raffaele and Roby 1977, Bond 1993). Beyond this, little useful information exists for comparison among species.

Despite its widespread distribution over the island of Puerto Rico, reductions in range and overall population of the Puerto Rican Bullfinch (hereafter bullfinch) are suspected (García et al. 2005). Studies of this species are needed to improve upon knowledge of its life history, as well as factors that may be contributing to population declines. Our objectives were to describe characteristics of the breeding biology of the bullfinch and to estimate its nest survival, a parameter that may vary with factors such as time, nest stage, nest height, precipitation, and resource availability. Annual variation in nest survival may result from factors such as fluctuations in predator numbers and changes in regional weather patterns (Dinsmore et al. 2002). Temporal shifts in predator communities, weather patterns, changes in behaviors of adults and young, and other factors may contribute to variation in nest survival within seasons (Klett and Johnson 1982, Grant et al. 2005). Stage-specific differences in nest survival may be observed because parental behavior, and thereby conspicuousness of nests, can change with stage (Best and Stauffer 1980, Martin et al. 2000). Nest placement may influence nest survival by

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causing variation in predation risk in relation to how accessible nests are to predominant nest predators of the habitat (Filliater et al. 1994, Schmidt et al. 2008). Precipitation may influence resource availability, alter nest predator foraging behavior (Morrison and Bolger 2002), or prohibit adults from foraging adequately for themselves or nestlings.

Although the diet of the bullfinch is varied, it is a primarily frugivorous species and appears to prefer fruit when it is available (Wetmore 1916, Pérez-Rivera 1994, Carlo et al. 2004). The diet of nestling bullfinches is unknown, but most frugivorous bird species feed large quantities of animal matter to their young, especially during the early portion of the nestling stage (Breitwisch et al. 1984). As nestlings gain the ability to thermoregulate, their protein demand typically decreases and parents transition into provisioning a greater proportion of fruit. Therefore, it is likely that nestling bullfinches are fed insects initially but are also fed fruit to some extent. The availability of fruit resources could then affect nest survival by influencing adult condition and behavior, such as the time spent away from the nest while foraging (Crawford et al. 2006, Boulton et al. 2008). To a lesser extent, fruit availability also probably influences what and how much nestlings are fed, as well as predator behavior (Schmidt 1999). For example, nest predators with an omnivorous diet may spend more time searching for nests, or come across more nests by chance, when fruit resources are lower.

Here we report nesting habits and nest survival of the bullfinch from two breeding seasons in southwestern Puerto Rico. This information will increase our understanding of the breeding ecology of an endemic passerine and will ultimately aid future studies and conservation efforts for this and other species in the subtropical dry forests of Puerto Rico.

METHODS

Study Area.—We studied Puerto Rican Bullfinches in two coastal tracts of subtropical dry forest (Ewel and Whitmore 1973) in southwestern Puerto Rico: Guánica State Forest (17° 58′ N, 66° 52′ W; hereafter Guánica) and La Jungla (17° 57′ N, 66° 57′ W; Fig. 1). From 1955–2010, these sites received, on average, 790 mm of rain per year (National Climatic Data Center 2010), but inter-annual variation is high and droughts occur regularly (Ewel and Whitmore 1973). The region is characterized by a distinct dry season from December to April, and a wet season spanning approximately late April to June or July, with another peak in rainfall from September to October (Faaborg 1982). The short, dense forests grow on shallow limestone soils that have little capacity for retaining water (Ewel and Whitmore 1973). Most of the 4,015-ha Guánica tract has been protected since 1919 with peripheral units added later (Colon and Lugo 2006). The forest is recognized as one of the highest quality remaining subtropical dry forests in the world (Lugo et al. 1996). Approximately half the reserve is mature, uncut vegetation; the other half consists of second-growth in various stages of regeneration (Lugo et al. 1996). The La Jungla tract, consisting of about 615 ha, is 8 km west of Guánica. It has been protected since approximately 2000 as a disjunct tract of the Guánica reserve. Much of the vegetation is in earlier stages of succession, with less mature forest overall, compared to Guánica (ANMW, pers. obs.). The land-use history of the sites includes charcoal production, grazing, subsistence agriculture, tree plantations (mostly *Swietenia mahogoni*) and logging, and human residential areas and roads (Lugo et al. 1996, Colón and Lugo 2006, Pérez-Martínez 2007).

Nest Survival.—We searched for and monitored bullfinch nests from April–July of 2009 (Guánica) and 2010 (Guánica and La Jungla). Nest searching efforts were focused in four discrete 25-ha plots in Guánica and in a single 100-ha plot in La Jungla, but we also monitored nests found opportunistically outside of these defined plots. In both sites, nest plots encompassed a range of forest ages. We monitored nests approximately every 3–5 days and determined if each nest failed (did not fledge any young) or succeeded (fledged $\geq$1 young). We checked nests above head height using either a small mirror or a plumbing camera attached to a telescoping handle. When a nest failed, we attempted to determine cause of failure, such as destroyed eggs and nest or an empty nest (indicating predation), or cold eggs or dead nestlings (indicating abandonment). After each nest failed or succeeded, we measured the height of the nest from the ground to the top of the nest rim to the nearest 0.1 m, and height and width to the nearest 0.1 cm.

Precipitation.—We used daily precipitation data collected from two locations, one corresponding with each site. For Guánica, we used data collected at a location central to the nest

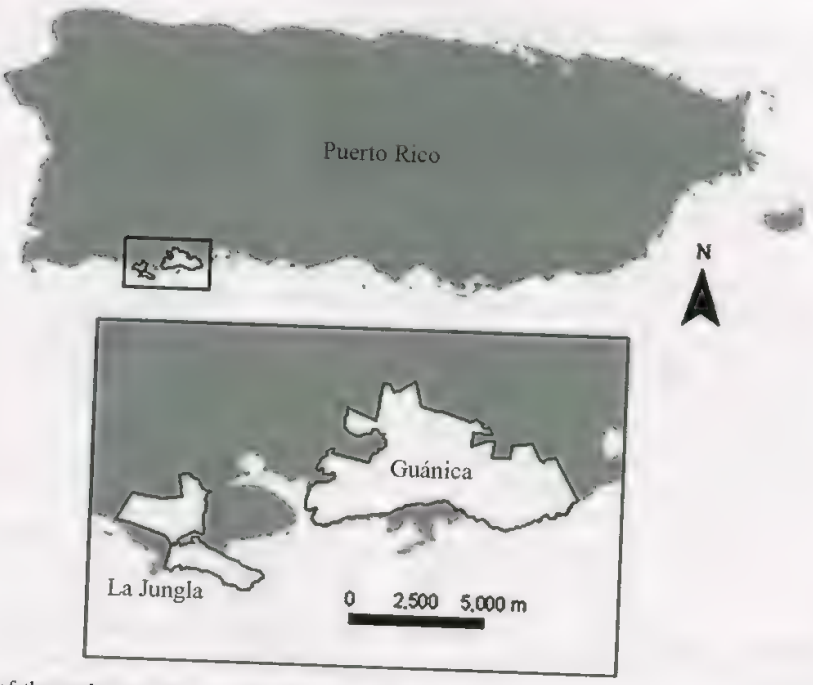

FIG. 1. Map of the study area. The inset map indicates the two study sites, La Jungla (17° 57′ N, 66° 57′ W) and Guánica (17° 58′ N, 66° 52′ W), and the location of each within southwestern Puerto Rico.

searching plots, courtesy of the DNER (M. Canals, pers. comm.). For La Jungla we used data from a U.S. Weather Bureau station in the town of Ensenada, approximately 4 km east of the La Jungla site (National Climatic Data Center 2010).

Fruit Abundance.—We systematically established 20 fruit monitoring stations at Guánica (five in each of the four nest plots) and 18 fruit monitoring stations at La Jungla to measure fruit abundance during the 2009 and 2010 breeding seasons. No known comprehensive list of fruit species consumed by the Puerto Rican Bullfinch exists. Most studies of frugivory in the bullfinch have occurred in wetter forests of Puerto Rico (Cruz 1980, Saracco 2001, Carlo et al. 2004), but see Pérez-Rivera (1994). Because plant species turnover is high between different habitats, foraging observations in wet forests are not very useful for developing a list of species consumed in the dry forest. Therefore, we had to rely on personal observations along with several publications to develop a list of 46 species of fruiting trees and cacti known or likely to be consumed by the bullfinch (Wetmore 1916; Lack 1976; Pérez-Rivera 1994; A. Morales Pérez, pers. comm.; J. Sustache, pers. comm.; and ANMW, pers. obs.).

Fruit monitoring stations were circular plots (Denslow et al. 1986, Loiselle 1987) of 7 m in diameter. We determined this plot size after preliminary surveys suggested that it would be an appropriate sampling area considering the average density of focal species and time required to conduct fruit counts. We marked up to five trees or cacti of at least 1.5-m height of each focal species at each station. If more than five individuals of a species were present, we marked only the five nearest to the center of the station. We visited stations weekly and visually estimated the number of ripe and unripe fruits on each marked individual. Fruit was considered ripe if it was completely mature and unripe if it was completely or partially immature. Each individual was then assigned a separate ripe and unripe fruit abundance index (FAI) based on the following logarithmic scale: 0 = no fruit, 1 = 1–10 fruits, 2 = 11–100 fruits, 3 = 101–1,000 fruits, and 4 = 1,001–10,000 fruits (following Saracco 2001). Although ripe fruits are preferred (ANMW, pers. obs.) and we were interested primarily in the ripe fruit abundance, we also wanted to examine the relationship between total (ripe + unripe) fruit abundance because bullfinches were also observed eating unripe and partially ripened fruit.

Weekly FAIs were summed within each site and we used linear interpolation to provide a daily index at each site during the course of the breeding season. In 2009, fruit scoring was not initiated until early June. Missing values from May were replaced with the mean values over the rest of the season within a site and year.

Statistical Analyses.—We modeled the daily survival of nests of bullfinches, defined as the probability that a nest will survive a single day, using the nest survival model of Dinsmore et al. (2002) as implemented in program MARK (White 2007). This method uses a generalized linear modeling approach based on a binomial likelihood. Dates were scaled so that 5 May, the date the first nest was found in either year, was set as day 1. For each nest we also included the following explanatory variables: linear and quadratic time trends within year, year, nest stage (incubation or nestling), site, nest height, precipitation, ripe FAI, total (ripe + unripe) FAI, and observer visits. We used the logit link function to incorporate covariates in all models. No goodness-of-fit test is available for the nest survival models in program MARK (Dinsmore et al. 2002).

We used a hierarchical approach to build the list of candidate models. First, we addressed temporal trends in daily nest survival. We assessed temporal variation within season by fitting constant survival, linear time trend, and quadratic time trend models. To evaluate variation between 2009 and 2010, we modeled year effects. We also fit a model to nest stage (incubation or nestling) to evaluate potential differences in survival between stages. Next, we modeled each individual covariate of site, nest height, precipitation, ripe FAI, total (ripe + unripe) FAI, and observer effects. Preliminary analyses suggested that total FAI models performed better than ripe-only FAI models; therefore, we only used total FAI scores in subsequent models. Finally, we added the competitive (ΔAIC < 2) time trend models to each of the individual covariates.

We ranked the set of candidate models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Akaike 1973) and Akaike model weights (w_i; Burnham and Anderson 2002) to select the most appropriate models for inference. Values reported in the results are means $\pm$ SE.

RESULTS

Nesting Biology.—Of 43 active bullfinch nests found during 2009–2010, 37 had sufficient data for nest survival analyses (Table 1). We monitored these nests for 220 exposure days across a 58-day interval (5 May–2 Jul). Of the 37 nests used in analyses, 29 failed during incubation, 5 failed during the nestling stage, 2 successfully fledged young, and 1 had an unknown fate. All unsuccessful nests appeared to have failed because of predation. We did not observe any evidence of nest abandonment, but we cannot exclude the possibility that abandonment occurred prior to predation in any failed nests. The two successful nests fledged 2 and 3 nestlings and were both in La Jungla in 2010. Both of these nests were located prior to the initiation of incubation and were observed on the day of fledging. The incubation period was 14 days and the nestling period was 14–15 days. During June 2010, one bullfinch nest at La Jungla was parasitized by a Shiny Cowbird (*Molothrus bonariensis*). The nest initially contained three bullfinch eggs and was later observed with one bullfinch egg and one Shiny Cowbird egg before it subsequently failed. Additionally, we were unable to determine what adult bullfinches were feeding nestlings, as the nesting adults tended to be extremely secretive. We attempted to observe nests from a distance, but the thick vegetation of the dry forest obscured views and adults rarely returned to nests while observers were within sight.

Observed clutch sizes of bullfinches ranged from 2–4 eggs with a mean of 3.1 $\pm$ 0.6 ($n = 25$). Nests ranged from 0.9 to 6.0 m above the ground, with a mean height of 2.4 $\pm$ 1.6 m ($n = 43$). Nest structures were, on average, 160.6 $\pm$ 41.3 mm in height ($n = 27$) and 123.9 $\pm$ 21.3 mm wide ($n = 25$). They varied in shape ranging from open cups to domed nests with side entrances. Nests were usually constructed of dry palm fronds (*Leucothrinax morrisii*), lignified vascular tissue of cacti (*Cephalocereus* spp.), and leaves and vines. Additionally, the thin, papery bark of *Bursera simaruba* was frequently used as a lining in the cup of the nest or in between layers of the nest structure.

During May and June 2009, we observed cooperative breeding behavior in bullfinches in Guánica. On several occasions we observed family groups consisting of two adults and 1–3 juveniles, where juveniles were observed collecting nesting material along with adults and on several occasions were seen adding material to nests. In two territories, we also observed three bullfinches, all in adult plumage, collecting nest

TABLE 1. The total number of nests of Puerto Rican Bullfinches (*Loxigilla portoricensis*) from two subtropical dry forest sites (Guánica and La Jungla) in southwestern Puerto Rico during 2009–2010 used in nest survival analyses.

Year	No. nests	Guánica		La Jungla	
		Incubation	Nestling	Incubation	Nestling
2009	9	9	2	–	–
2010	28	4	0	23	6
Totals	37	13	2	23	6

material together. No additional cooperative behavior such as feeding nestlings was observed, and no cooperative behavior was observed in 2010.

Nest Survival.—In the first step of analysis, all time trend models were competitive (<2 ΔAIC_c; Table 2). Therefore, each of these models was combined with individual covariates. Ten resulting models were competitive and provided approximately equal support for constant and quadratic time trends in nest survival over the season (Table 2). The top model, although weak and insignificant, does suggest that fruit availability has a positive relationship with nest survival ($\hat{\beta}_{FAItotal}$ = 0.007, SE = 0.004, 95% CL = −0.001, 0.015). Similarly, the variables site and precipitation each show weak, positive relationships with nest survival in two of the top models. Nest height, conversely, shows a weak, negative relationship with nest survival. Linear time trend, stage and year effects were not well supported in our models and there was little evidence of observer effects on nest survival. Under the top model, daily nest survival rates for each site and nest stage ranged from 0.83–0.86% in 2009 and 0.80–0.93% in 2010. Nest success was 0.012 (95% CL = 0.001, 0.071) for Guánica in 2009, and 0.044 (95% CL = 0.007, 0.147) for La Jungla in 2010. We defined nest success as the probability of surviving a consecutive 14-day incubation period and a 14-day nestling period, beginning 24 May (the mean date of initiation of incubation in both years) and using mean values for all covariates. Nest success could not be estimated for Guánica in 2010, because we had no nestling stage data from that site and year.

DISCUSSION

This study has provided valuable information about the breeding biology of the Puerto Rican Bullfinch in southwestern Puerto Rico, including estimates of the length of the incubation and nestling periods and a preliminary description of cooperative breeding behavior in juvenile or helper bullfinches. Additionally, this research has produced the first estimates of nest survival for the bullfinch and shed light on several factors that may influence the species' nest survival. It is important to note that, because of our small sample sizes and lack of strong results, we are not making inferences about direct causes of nest mortality; instead, we are interested in examining patterns in nest survival.

Most or all nest failure observed during this study resulted from predation. Other studies have reported low estimates of nest survival or success in the tropics (Ricklefs 1969, Skutch 1985, Robinson et al. 2000, Ryder et al. 2008, Newmark and Stanley 2011), and in particular that nest predation is often the most important cause of nest loss in the tropics (Sargent 1993, Martin 1996). We think the most frequent nest predator in Guánica and La Jungla was the Pearly-eyed Thrasher (*Margarops fuscatus*). This omnivorous species is an avid nest predator, and has been observed depredating bullfinch nests (Arendt 2006). We also observed one bullfinch nest in Guánica as it was detected by a Pearly-eyed Thrasher, and soon after it was found to be depredated (ANMW, pers. obs.). Other potential, although less probable, nest predators occurring at Guánica and La Jungla include Red-legged Thrushes (*Turdus plumbeus*; Oberle 2000); Puerto Rican racers (*Borikenophis portoricensis*; Pérez and Laboy 1996); anole lizards (*Anolis* spp.), one of which was observed depredating the nest of a Bananaquit (*Coereba flaveola*) during our study (ANMW, pers. obs.), small Indian mongoose (*Herpestes javanicus*; Vilella 1998), green iguanas (*Iguana iguana*; Lazell 1973), feral cats (*Felis catus*) and black rats (*Rattus rattus*; Woodworth 1999, Arendt 2000).

Assumptions of the nest survival model in MARK are that nests can be correctly aged, nest fates are correctly determined and are independent, daily survival rates are homogeneous, and nest

TABLE 2. Models considered for analyzing daily nest survival for Puerto Rican Bullfinches (*Loxigilla portoricensis*) with corresponding number of parameters (K), ΔAIC_c values, and Akaike weights (w_i) for model selection. The table illustrates the hierarchical approach to model building. In the first step, time trend models were considered. The AIC_c value for the top-ranked time trend model was 128.65. In the next step, individual covariates were modeled and competitive time trends were combined with individual covariates. The AIC_c value for the top-ranked time trend + covariate model was 127.96. Only competitive ($<2\Delta AIC_c$) models are presented. Analyses were based on 220 days of nest monitoring at 37 nests in two subtropical dry forest sites in southwestern Puerto Rico during 2009–2010.

Model	ΔAIC_c	w_i	K	Deviance
Time Trend Models				
Constant	0.00	0.29	1	126.63
Quadratic	0.28	0.26	3	122.83
Year	0.88	0.19	2	125.48
Linear	1.42	0.14	2	126.02
Stage	1.85	0.12	2	126.45
Best Time Trends + Covariates				
Constant + Total FAI	0.00	0.09	2	123.91
Quadratic + Site	0.59	0.07	4	120.39
Constant + Site	0.61	0.07	2	124.52
Constant + Precipitation	0.94	0.06	2	124.84
Quadratic + Precipitation	1.32	0.05	4	121.11
Constant + Height	1.44	0.05	2	125.34
Constant + Ripe FAI	1.71	0.04	2	125.62
Quadratic + Total FAI	1.82	0.04	4	121.61
Linear + Total FAI	1.94	0.04	3	123.80
Quadratic + Height	1.95	0.04	4	127.75

discovery and monitoring do not influence survival. We did not model the effects of age, because several nests could not be accurately aged. The other assumptions were met appropriately, as nest fates were usually easily determined, nests were dispersed over the landscape sufficiently to assume independence, and estimated survival rates were assumed to apply equally among nests. The final assumption, that nest checks do not influence survival, was of concern because nest failure rates were so high. Although most studies have found no significant effects of nest checks (e.g., Nichols et al. 1984), others have provided evidence that disturbing nests during nest checks may provide cues or enhance existing cues used by predators to find nests (e.g., Westmoreland and Best 1985). We tested for a change in nest survival in the interval following a visit to a nest by modeling nest visits as individual covariates in MARK; this model was poorly supported and suggests that nest checks did not influence survival in our study. Additionally, it is important to note that we were unable to incorporate daily nest survival estimates during the egg-laying stage into our overall estimate of nest survival, because we had little data from this stage. Therefore, our nest survival estimates are probably biased high because they only include the incubation and nestling stages.

Top nest survival models primarily provided support for constant and quadratic time trends; therefore, it is unclear if there was a predominant time trend in nest survival in 2009 and 2010. Although a large number of nest survival models received approximately equal support and no covariates were statistically significant, the results seem biologically appropriate and would likely be strengthened with larger sample sizes and more years of data. Collectively, the top models suggest that available fruit is important for successful nesting, increased precipitation is related to higher nest survival, nest survival was higher at La Jungla than at Guánica, and increased nest height is related to lower nest survival.

The positive relationships between nest survival and the variables precipitation and fruit availability were unsurprising. Increased precipitation was probably related to increased resource availability, whether fruit resources or other resources that we did not measure, such as insect abundance. Both total and ripe FAIs showed weak positive trends

in relation to nest survival. However, total FAI was better supported than ripe FAI, indicating that including the abundance of unripe fruit in addition to ripe fruit is an important consideration when assessing resource availability for bullfinches. A significant relationship between fruit abundance and nest survival may have been less detectable, because nest failures were all or nearly all due to predation rather than starvation or abandonment and because we had very small sample sizes for the nestling stage, the stage in which we expect survival to be most affected by resource availability. Furthermore, fruiting is spatially and temporally ephemeral in the dry forest, and some fruit species may only be important to birds in some seasons or years (Blake et al. 1990). This emphasizes the need for more years of nest survival and fruiting phenology data. Finally, less inference can be made between nest survival and fruit abundance in 2009, because there were missing values in that year.

During 2010, nest survival was slightly higher at La Jungla than Guánica. These sites are only 8 km apart, are both coastal forest tracts, and experience similar weather conditions. Although the vegetation is shorter and scrubbier at La Jungla, both sites are characterized by the same general forest structure and nearly the same plant species composition. Two notable differences between La Jungla and Guánica were in amounts of fruit produced and density of Pearly-eyed Thrashers. Weekly fruit scores were consistently lower at Guánica even though the average number of trees per fruit station was similar between sites (ANMW, unpubl. data). However, as the relationship between FAI and nest survival was weak, we can only suggest that the lower fruit abundance at Guánica may have negatively impacted nest survival. Additionally, Pearly-eyed Thrashers were infrequently captured in mist nets and detected by point count surveys in La Jungla compared to in Guánica (Kornegay 2011). The much lower density of Pearly-eyed Thrashers in La Jungla may have contributed to higher survival of bullfinch nests at that site. Finally, our results suggest that higher nests had slightly lower nest survival. This might indicate that the Pearly-eyed Thrasher searches for nests higher in the canopy.

Despite the low nest survival observed in this study, bullfinches persist in southwestern Puerto Rico. This suggests that the species has a relatively high adult survival rate, as is widely assumed for tropical birds (e.g., Ricklefs 1969, 1997, Johnston et al. 1997). Indeed, a long-term mist netting study in Guánica reports that the annual apparent survival of adults from 1989–2011 was 0.75 (Faaborg and Wiewel 2010). Furthermore, the Guánica study has produced several age records for bullfinches that are 9–12 years old (Faaborg and Wiewel 2010), which is relatively long-lived for small passerines. It should also be noted that we found and monitored only a small subset of the total bullfinch nests in our study areas. Although we observed very few fledglings produced from nests that we monitored, hatch-year bullfinches were regularly captured in both years during a concurrent mist-netting study that took place within our nest plots (Kornegay 2011). Bullfinch nests vary in detectability, and it is likely that our sample was biased towards nests that were more detectable to both nest predators and human observers. This may have contributed to higher predation rates in our sample than in the overall population of bullfinch nests.

Wetmore (1916:124) reported that bullfinches "nest rather irregularly throughout the year." This observation may be the result of recording nests throughout most of the year in the wetter forests of Puerto Rico, where seasonality is much less pronounced. In the dry forests of southwestern Puerto Rico, most species restrict their breeding to the spring and early summer rainy season of approximately late April to July. During the dry season from December to April, resources are probably too limiting for birds to successfully rear young in most years. However, we think that bullfinches do breed opportunistically in the dry forest as well. For example, in January–March 2009, juvenile bullfinches were regularly captured in mist nets (J. Toms, pers. comm.) and multiple family groups including juvenile bullfinches were observed (ANMW, pers. obs.). Several rainfall events, including one unusually large event, occurred in January 2009, which probably initiated this breeding activity. It might be possible that bullfinches and other species attempt to breed again during the shorter annual rainy peak in September and October. Considering the adult survival rates and longevity of bullfinches, it is not surprising that these birds may be able to breed when conditions are favorable and perhaps forego breeding when conditions are less suitable.

The bullfinch is not thought to be a frequent victim of nest parasitism by Shiny Cowbirds (Post et al. 1990, Nakamura and Cruz 2000). In the only other known report of parasitism of a bullfinch

nest, Cruz et al. (1989) observed parasitism of one bullfinch nest out of four monitored in southwestern Puerto Rico from 1980–1983. The Lesser Antillean Bullfinch and Barbados Bullfinch have also been observed victims of Shiny Cowbird parasitism (Friedmann 1943, ffrench 1973), although it is likely an infrequent occurrence in these species as well. Therefore, parasitism by Shiny Cowbirds is probably not a significant factor in nest survival of the bullfinch.

The cooperative breeding behavior we observed in 2009 in Guánica was restricted to nest material collection and nest building by helper bullfinches. These birds were likely young produced by the associated adult pair during the previous breeding occasion (Stacey and Koenig 1990). No further cooperative breeding behavior was observed, but it should be noted that bullfinches are secretive breeders and were infrequently observed building or incubating, and never observed feeding nestlings. Therefore, we do not know if helpers contributed to additional breeding efforts. This behavior was only observed in 2009, following the rainy January that seemed to have initiated early breeding in bullfinches that year. Cooperative breeding behavior is observed more frequently in non-migratory species, species with low annual mortality rates, and species living in relatively unchanging environments (Arnold and Owens 1998, Cockburn 2006), all of which are characteristics of bullfinches. Additionally, cooperative breeding is considered a facultative trait in most bird species (Hatchwell and Komdeur 2000) and may not occur every year, or in all breeding pairs or habitats, in bullfinches. Cooperative breeding has been inferred to occur in 9% of species of the family Emberizidae (Cockburn 2006).

The results presented here shed light on the life history of a relatively long-lived tropical island endemic, the Puerto Rican Bullfinch, in southwestern Puerto Rico. We emphasize the need for additional research on the breeding biology of the bullfinch. Additional nest survival studies would increase sample sizes and yield information on nest survival over a variety of weather conditions, which seems particularly important for the highly seasonal and drought-subjected southwestern region of Puerto Rico. Foraging studies would help confirm which fruit and insect species are consumed by bullfinches in the dry forest and would aid in developing more detail-specific nest survival studies. As nest predation was our most frequent cause of nest failure, it may be useful to quantitatively determine which nest predators play the most important roles in depredating bullfinch nests.

Dry forests of southwestern Puerto Rico historically supported higher bird densities and species diversity than the wetter forests of the island (Kepler and Kepler 1970). Because Guánica is considered one of the most pristine tracts of dry forest remaining in the subtropics (Lugo et al. 1996), we expect that nest survival rates should be relatively high. There is a clear need for determining if the low nest survival rates we observed are typical or if they may be playing a role in suspected and known population declines in the bullfinch and other Puerto Rican endemics (García et al. 2005). No apparent, significant changes in the habitat in Guánica have occurred within the past few decades (Faaborg et al. 2013). This suggests that impacts on nest survival might be occurring at a larger scale, such as through climate change, lack of disturbance to forest habitat, or habitat loss in the matrix surrounding our study area.

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SEASONAL USE OF HABITAT BY SHRUB-BREEDING BIRDS IN A SOUTHEASTERN NATIONAL FOREST

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ABSTRACT.—Populations of shrub-breeding birds are declining in eastern North America, and loss of habitat has been implicated in these declines. Seasonal use of habitat by shrub-breeding birds in the southeastern US remains understudied despite the fact that it is well documented that species resident within a region can shift habitat use dramatically between seasons. To better understand year-round habitat occupancy by shrub-breeding birds, we conducted bird counts and vegetation surveys during summer and winter 2008–2009 within Tuskegee National Forest, Alabama. We used multi-season occupancy models to examine use of habitat and to contrast seasonal occupancy patterns of four species of resident shrub-breeding birds—Brown Thrashers (*Toxostoma rufum*), Eastern Towhees (*Pipilo erythrophthalmus*), Northern Cardinals (*Cardinalis cardinalis*) and Carolina Wrens (*Thryothorus ludovicianus*). Brown Thrashers and Eastern Towhees are partially migratory—meaning some populations have separate breeding and wintering areas—whereas Carolina Wrens and Northern Cardinals are non-migratory. All four species showed seasonal changes in use of habitat between summer and winter, and all species were associated with both vegetation structure and certain types of cover. Further, partially migratory shrub-breeding species had greater site-turnover and increases in occupancy between summer and winter than non-migratory species. Our results suggest that: (1) management actions based on breeding habitat requirements will likely not create suitable winter habitat, and (2) management of resident shrub-breeding birds will require not only the creation and maintenance of certain types of cover, but also certain structural aspects of vegetation within habitats. *Received 1 March 2013. Accepted 23 August 2013.*

Key words: early successional habitats, Gulf Coastal Plain, multi-season occupancy analysis, shrub-breeding birds, shrubland, wildlife opening.

Use of habitat by birds is likely to change between breeding and non-breeding periods because of seasonal changes in resource availability and vegetation structure as well as constraints on birds to find suitable nest sites during summer (e.g., Bilcke 1984, Morrison et al. 1986, Keller and Yahner 2007). For instance, many migratory species will switch from using scrub during the breeding season to forested habitat in the winter, and vice-versa (Robbins et al. 1989). Therefore, a complete understanding of the habitat requirements of a given species can be achieved only through a multi-season perspective.

As a group, shrub-breeding birds are in decline because of habitat loss resulting from changes in agricultural practices, maturation of forests, and urbanization (e.g., Askins 1993, Dettmers 2003, Murphy and Moore 2003). Despite calls for the creation and preservation of habitat for shrub-breeding birds in the eastern US (e.g., Woodrey et al. 1998, Askins 2001, Dettmers 2003), the specific habitat requirements of most shrub-breeding birds remain poorly understood. Most studies of habitat use by shrub-breeding species focus on the breeding season (e.g., Chandler et al. 2009, King et al. 2009a, Schlossberg et al. 2010), and the use of habitat by shrub-breeding birds during winter remains poorly known (Schlossberg and King 2007).

A seasonal approach to studies of habitat use by shrub-breeding birds is especially needed in the southeastern US. Populations of shrub-breeding birds in the northeastern US and southeastern Canada have experienced the most drastic declines (e.g., Askins 1993, Hagan 1993, Sauer et al. 2008), and many of these species, such as the Brown Thrasher (*Toxostoma rufum*) and Eastern Towhee (*Pipilo erythrophthalmus*), winter in the southeast (Hagan 1993, Schlossberg and King 2007). Therefore, knowledge of seasonal habitat use by shrub-breeding birds within the southeast can inform the management of populations that breed elsewhere.

Site selection by birds is considered a hierarchical process with birds first selecting the type of cover in which to settle and then choosing specific sites with preferred structural aspects of vegetation (e.g., Johnson 1980, Hutto 1985, Hagan and Meehan 2002). Therefore, investigations into use of both cover-type and vegetation structure are

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needed to accurately describe the habitat needs of birds (Wiens 1989, Knick and Rotenberry 1995). A previous study of migratory birds wintering within the same study site surveyed here for scrub birds found that models including information regarding both cover-type and vegetation structure out-performed models which included either scale alone (McClure et al. 2012). A multi-scale approach to studies of habitat use by shrub-breeding birds may be especially important because shrub-nesting birds have clear preferences for certain types of cover (e.g., Bulluck and Buehler 2006, Fink et al. 2006, King et al. 2009b), and their life-history makes them inherently dependent on certain structural aspects of vegetation for nesting, cover, and foraging (e.g., Hagan and Meehan 2002, MacFaden and Capen 2002, Schlossberg et al. 2010).

Although shrub-nesting birds are generally considered to prefer early successional types of cover such as clearcuts and beaver meadows (e.g., Greenberg et al. 1995, Bulluck and Buehler 2006, Chandler et al. 2009), many will use forested areas with appropriate vegetation structure (Engstrom et al. 1984, Hamel 1992, Schlossberg and King 2007). We conducted bird counts and surveys of vegetation during summer and winter across a forested matrix in the Southeast that contained several types of early successional habitat. We contrasted the occupancy patterns and habitat use of four resident—i.e., present year-round—shrub-nesting species that represent two different situations. Northern Cardinals (*Cardinalis cardinalis*) and Carolina Wrens (*Thryothorus ludovicianus*) are non-migratory (Dow and Scott 1971, Taylor et al. 1983) and their populations have increased significantly range-wide since the 1960s (Sauer et al. 2011), whereas Brown Thrashers and Eastern Towhees are partially migratory—having some populations that breed in the northeast US and winter in the southeast, and other populations that remain in the same region year-round (Hagan 1993, Schlossberg and King 2007)—and have significantly declining populations (Sauer et al. 2011). We predicted that partial migrants would show greater changes in occupancy and higher rates of site-turnover between summer and winter than the non-migrants, that patterns of habitat use would differ for all species between seasons, and that all species would be associated with aspects of habitat at multiple scales.

METHODS

Study Area.—Our study site was centered on the Tuskegee National Forest (TNF) in Macon County, Alabama (32° 25.899′ N, 85° 38.637′ W). This area contained a range of habitats including several early successional habitats such as clearcuts, old fields, wildlife openings and beaver meadows, as well as native hardwood and pine forests (Table 1). Management units within TNF are burned every 2–5 years. We conducted bird surveys at locations within the southwest portion of the national forest (Fig. 1) which were previously established to examine the effects of bird communities on virus transmission (Jacob et al. 2010, Estep et al. 2011, Estep et al. 2012). Survey locations were in a systematic grid, and were not biased toward any particular type of cover. All survey points were roughly 250 m from the next nearest point.

Surveys of Breeding Birds.—Four trained observers conducted surveys of breeding birds at 338 bird survey locations in 2008. We conducted point counts (Ralph et al. 1995) following the protocols of Hamel (1992) and recommendations of Mackenzie and Royle (2005). During a point count, we recorded all birds detected by sight or sound within a 100-m radius, excluding flyovers. Observers also recorded weather variables hypothesized to affect detection of birds such as cloud-cover, temperature and wind speed. Using this protocol, each point was surveyed on two different dates and at two different times of day. We conducted three consecutive 4-min counts during each round of surveys. We rotated observers between rounds to ensure two different observers surveyed each point and that each observer conducted approximately the same number of surveys in each cover-type. All surveys were conducted between 15 May and 31 June and between 0500–1100 CDT.

Surveys of Winter Birds.—Three trained observers conducted winter point counts at 205 of the summer bird survey sites within Tuskegee National Forest from 28 January through 28 February 2009 between 0600–1400 CST according to the recommendations of Rollfinke and Yahner (1990). Point counts lasted 20 mins and were divided into 4-min intervals during which we recorded all birds detected within 100 m, excluding flyovers. Survey locations were only visited once. However, we were careful to ensure that each observer conducted surveys within each

TABLE 1. Models tested regarding the use of habitat by resident shrub-breeding birds at both the cover-type and vegetation scales as well as the sources of the hypothesis for each model.

	Model	Source of hypothesis
Cover-type	Canopy cover	(MacArthur and MacArthur 1961, Shugart and James 1973)
	Development	(Beissinger and Osborne 1982, Oneal and Rotenberry 2009, Bried et al. 2011)
	Clearcuts	(Conner et al. 1979, Thompson et al. 1992, Greenberg et al. 1995)
	Hardwoods	(Dickson 1978, Sallabanks et al. 2000, Bowen et al. 2007)
	Floodplain	(Dickson 1978, Sallabanks et al. 2000, Bowen et al. 2007)
	Natural Pine	(Engstrom et al. 1984, Allen et al. 2006, Bried et al. 2011)
	Wildlife Openings + Agriculture	(Schlossberg and King 2007, King et al. 2009b, Johnson 2010)
	Development + Agriculture + Scrub	(Hamel 1992, Murphy and Moore 2003, Schlossberg and King 2007)
Vegetation	Basal Area	(Schlossberg and King 2007, Chandler et al. 2009, Schlossberg et al. 2010)
	Grass Layer Density	(Schlossberg and King 2007, Chandler et al. 2009, Schlossberg et al. 2010)
	Canopy Cover	(MacArthur and MacArthur 1961, Shugart and James 1973)
	Midstory Density	(Schlossberg and King 2007, Chandler et al. 2009, Schlossberg et al. 2010)
	Shrub Density	(Schlossberg and King 2007, Chandler et al. 2009, Schlossberg et al. 2010)
	Ground Cover + Leaf Litter	(Hamel 1992, Schlossberg and King 2007)
	Canopy Cover + Leaf Litter	(Hamel 1992, Schlossberg and King 2007)
	Ground Cover + Grass layer Density + Midstorey Density + Basal Area	(MacArthur and MacArthur 1961, Hamel 1992, Schlossberg and King 2007)

cover type within our study site, thus reducing potential observer bias. Our protocol of counting birds within a 100-m radius is supported by previous research demonstrating that data collected using a count radius of 100-m produces well-performing models of habitat use by wintering birds within our study site (McClure et al. 2012). We also recorded weather variables hypothesized to influence detection.

Surveys of Vegetation.—We measured vegetation structure within 16-m radius plots centered on bird survey points (Anderson and Shugart 1974, La Sorte et al. 2009). We quantified canopy cover by taking densitometer readings at 4-m intervals along 16-m transects in all cardinal directions from the center (Robinson 1947). We quantified depth of leaf litter at the ends of the transects (Ortega and Capen 1999). We measured the density of vegetation using a modified, 12-m Robel pole placed in the center of the plot (Mills et al. 1991). The pole was painted with alternating 10-cm black-and-white stripes. We quantified density of vegetation at 0–0.6 m, 0.6–4.6 m, 4.6–7.6 m, and 7.6–12 m (MacArthur and MacArthur 1961) by calculating the percentage of stripes obscured by vegetation within each interval. Observers recorded pole measurements from the edge of the plot in all cardinal directions. We also measured diameter at breast height (dbh) of all trees >10-cm dbh within the plots during 2008–2009. Plots were only surveyed once for dbh measurements, because we assumed they would remain unchanged between seasons. Diameter at breast height measurements were taken during 2008–2009. All other vegetation measurements were conducted concurrent with bird surveys and separate vegetation measures were collected during breeding and wintering seasons. Because of logistical constraints we were only able to survey vegetation and birds at 89 sites during both summer and winter.

Land Cover.—We quantified percentage of each cover-type within 100-m radius buffers drawn with ArcGIS (ESRI 2008) using the Alabama Gap Analysis Program Land Cover Map (Kleiner et al. 2007). We combined similar landcover classes following McClure et al. (2011). For instance, pixels classified as pasture and row crop were combined to form a broader agricultural classification and, low-intensity, medium-intensity, high-intensity developed areas and developed open spaces were combined to form a broad habitat class that we termed "developed." Successional scrub subclassifica-

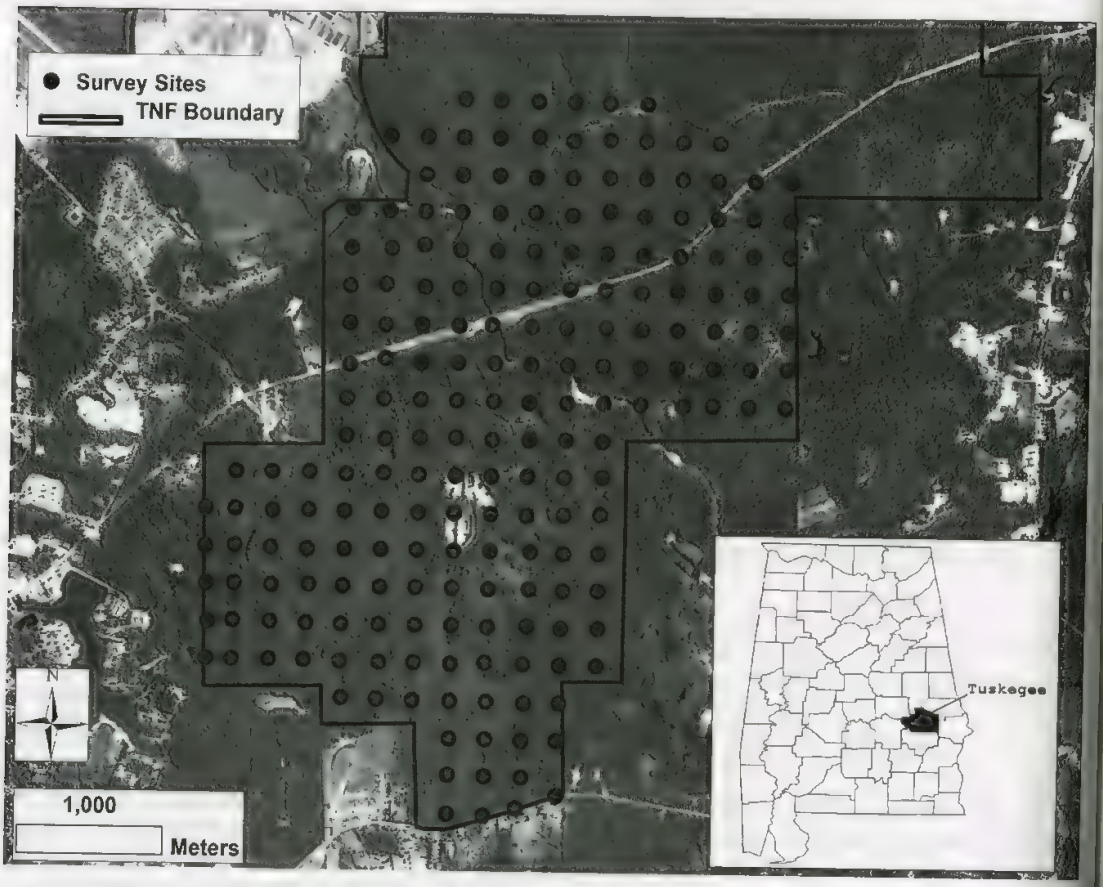

FIG. 1. Map of our study site within Tuskegee National Forest, Alabama. Only sites which were surveyed for birds in both summer and winter 2008–2009 are shown.

tions were combined to form a broad, scrub classification; floodplain and mesic slope forests were combined to form a hardwood classification; and, subclassifications of pine forests were combined to form pine and natural pine (which excludes plantations) classifications; (Table 2 in McClure et al. 2011). We also quantified the percentage of canopy cover within 100-m radius buffers using the National Landcover Database Tree Canopy Cover Map (Homer et al. 2004b). Both of the maps that we used to derive cover-type (Homer et al. 2004a, Kleiner et al. 2007) have a resolution of a 30-m pixel. Within our study site, successional habitats are found mostly within the land cover classifications of agriculture, successional scrub-other—which consists of wildlife openings—and, floodplain forest and water—which contain or surround beaver meadows. The only landcover classification indicating regeneration habitats is successional scrub-clearcut.

Analysis.—We restricted our analysis to species that were classified as successional or scrub breeders by Sauer et al. (2011) and that were detected during both summer and winter surveys. We used summer vegetation measurements for analysis of breeding habitat use, and winter vegetation measurements for analysis of habitat use during winter.

We used dynamic occupancy models to examine habitat use during both summer and winter (MacKenzie et al. 2003). Dynamic occupancy models allow calculation of initial occupancy (Ψ) and detection (p) as well as probability of colonization (γ) and vacancy (ε) between sampling occasions (MacKenzie et al. 2003).

We built occupancy models in a stepwise fashion—modeling one parameter at a time—in order to limit the number of models built (Olson et al. 2005). We first modeled summer detection, then winter detection. Next we modeled Ψ, γ, and

TABLE 2. Naïve breeding (ψ_b) and winter occupancy (ψ_w), estimated breeding ($\hat{\Psi}b$) and derived winter ($\hat{\Psi}w$) occupancy, and rate of turnover (τ) of resident shrub-breeding species within Tuskegee National Forest, 2008–2009. Breeding data were collected between 15 May and 30 June 2008; winter data were collected between 28 January and 28 February 2009. Standard errors are in parentheses.

Common name	Scientific name	Ψ_b	ψ_w	$\hat{\Psi}b$	$\hat{\Psi}b$	τ
Northern Cardinal	*Cardinalis cardinalis*	0.97	0.35	0.97 (0.02)	0.52 (0.10)	0.02 (0.03)
Carolina Wren	*Thryothorus ludovicianus*	0.73	0.53	0.78 (0.06)	0.67 (0.07)	0.14 (0.06)
Eastern Towhee	*Pipilo erythrophthalmus*	0.29	0.43	0.32 (0.06)	0.55 (0.08)	0.59 (0.08)
Brown Thrasher	*Toxostoma rufum*	0.03	0.06	0.03 (0.01)	0.12 (0.07)	1.0 (<0.01)

ε at the land cover scale, then the vegetation scale. At each step, we incorporated the most supported models from previous steps into subsequent models. Because we used consecutive sampling occasions, temporal autocorrelation between occasions was likely. To control for the possibility of temporal autocorrelation we also included a covariate indicating whether the species was detected in the previous occasion (t-1, Betts et al. 2008) in all models of detection. Because bird song rate is known to vary with stage of breeding (e.g., Wilson and Bart 1985), detection is likely to vary between seasons. We therefore also included a covariate indicating the season during which each observation was made in all models of detection. Although all of our observers were trained, professional ornithologists, it is possible that they differed in their ability to detect and identify birds. We therefore tested for observer effects by including dummy-coded covariates for observers. To simplify observer models and preserve degrees of freedom, if several observers had similar probabilities, they were lumped together and the model was re-run with the simpler structure. This protocol allowed us to test and control for effects of different detection abilities among observers. Models of detection were built using each covariate hypothesized to affect detection, separately. For each species, we ranked and compared all models of detection using Akaike's Information Criterion, (AIC, Burnham and Anderson 2002). We then incorporated the detection model with the lowest AIC into all models of Ψ.

When modeling Ψ, γ, and ε, we tested models containing combinations of covariates which we hypothesized *a priori* based on previously published studies would explain bird occupancy at both the vegetation and cover-type levels (Table 1). Models within $\Delta AIC < 2$ are considered to be the best models (Burnham and Anderson 2002) Therefore, for Ψ, γ, and ε at both the vegetation and cover-type levels, we based inference on models $\Delta AIC < 2$. Model selection using AIC favors the retention of covariates with 85% confidence intervals that exclude zero (Burnham and Anderson 2002, Arnold 2010), making 85% confidence intervals more consistent than 95% confidence intervals with model selection based on AIC (Arnold 2010). We therefore considered covariates with 85% confidence intervals that excluded zero and within models $\Delta AIC < 2$ which were ranked higher than the null as useful for inference. All data were analyzed using the package unmarked (Fiske and Chandler 2011) in R (R Development Core Team 2011). To avoid convergence problems inherent with small sample sizes and still obtain a biologically relevant sample, we only modeled parameters for which we had at least 10 observations. For instance, we only modeled colonization if at least 10 sites which were observed as occupied during winter were also observed as unoccupied during summer. Unmodeled parameters were held constant at the intercept.

We also assessed differences in occupancy between summer and winter by using the final model for each species to estimate summer occupancy and derive winter occupancy (MacKenzie et al. 2003, MacKenzie et al. 2006). We further derived estimates of turnover for each species. Regarding this study, turnover is defined as the probability that a site occupied during winter was not occupied the previous summer and is derived using the equation: $\tau = \gamma(1 - \Psi_w)/\Psi_s$ (adapted from Royle and Kéry 2007) where τ is turnover between summer and winter, Ψ_s is summer occupancy, and Ψ_w is winter occupancy. Turnover rates of 1 indicate that no sites occupied during winter were occupied during summer and rates of zero indicate that all sites occupied during winter were occupied during summer (Nichols et al. 1998). Turnover is therefore a measure of the

TABLE 3. The AIC-best model of detection for resident shrub-nesting birds. Values (β [SE]) for each covariate are shown as well as the model weight (w_i) for each model.

	Intercept	t-1	Winter	Date	Winter × Date	Observer	w_i
Northern Cardinal	4.53 (1.02)	1.07 (0.19)	−6.49 (1.27)	−0.03 (0.01)	0.05 (0.02)		0.82
Eastern Towhee	6.23 (2.04)	1.13 (0.28)	−10.63 (2.22)	−0.04 (0.01)	0.13 (0.03)		1
Brown Thrasher	−0.22 (0.44)	1.13 (0.63)	−2.01 (0.67)				1
Carolina Wren	−0.3 (0.16)	1.49 (0.21)	−0.77 (0.23)			−1.05 (0.26)	0.91

difference in the spatial pattern of occupancy between summer and winter (Nichols et al. 1998). We estimated standard errors of summer and winter occupancy as well as turnover using a parametric bootstrap with 1,000 iterations. Results are presented as coefficient values ± SE.

RESULTS

We detected Eastern Towhees and Carolina Wrens at enough sites to analyze use of both vegetation structure and cover-type during both summer and winter (Table 2). During summer, we detected Northern Cardinals at nearly every site (Table 2). Therefore, there was not enough variation in the data on Northern Cardinals for us to model summer occupancy or colonization. Brown Thrashers were not detected on enough sites at which vegetation surveys were conducted for us to analyze associations of habitat use with measurements of vegetation. We therefore analyzed use of habitat by Brown Thrashers using cover-type measurements at all sites that were surveyed for birds in both summer and winter. The only parameter for which we had enough data for Brown Thrashers was colonization (11 sites). Occupancy of Northern Cardinals and Carolina Wrens decreased between summer and winter, and occupancy of Brown Thrashers and Eastern Towhees increased (Table 2). Rates of turnover mirrored occupancy estimates with Northern Cardinals and Carolina Wrens having lower rates of turnover than Brown Thrashers and Eastern Towhees (Table 2).

The best model of detection for each species received most of the model weight (Table 3) of useful models. Detection of all species was affected significantly by season. Brown Thrashers and Carolina Wrens were both less detectable during winter, and one observer was less likely to detect Carolina Wrens. The interaction between the factor indicating winter surveys and date was useful for inference for both Northern Cardinals and Eastern Towhees indicating that detection of both species decreased over the summer and increased during the winter.

Every species was associated with certain types of cover. Covariates considered to be useful for inference indicated that Northern Cardinals were less likely to abandon sites surrounded by development (Fig. 1, Table 4, −7.41 ± 3.91). Habitat use of Eastern Towhees was characterized by an avoidance of hardwoods with summer occupancy negatively correlated with both floodplain (Fig. 1, Table 4, −1.44 ± 0.59) and hardwood forest (Fig. 1, Table 4, −1.59 ± 0.64). Colonization by Eastern Towhees was also negatively correlated with both floodplain (Fig. 1, Table 4, −1.47 ± 0.75) and hardwood forest (Fig. 1, Table 4, −2.06 ± 0.92). Carolina Wrens were more likely to occupy sites within floodplain forest during summer (Fig. 1, Table 4, 3.04 ± 2.09). Brown Thrashers were likely to colonize areas characterized as successional scrub-other—which consist mostly of wildlife openings in our study site—in the winter (Fig. 1, Table 4, 6.59 ± 3.16).

Associations with vegetational structure during both seasons reveal further habitat selection once birds settle within a cover-type. Carolina Wrens were more likely to abandon sites with dense vegetation >7.6 m tall during winter (Fig. 2, Table 4, 5.56 ± 2.58), and less likely to abandon sites with dense ground cover (Fig. 2, Table 4, 5.69 ± 2.99) and high basal area (Fig. 2, Table 4, 1.35 ± 0.83). Ground cover was important for site use of Eastern Towhees during both summer and winter with summer occupancy being negatively associated with ground cover (Fig. 2, Table 4, −2.81 ± 1.84) and dense vegetation >7.6 m tall (Fig. 2, Table 4, −2.81 ± 1.84). Eastern Towhees were more likely to colonize sites with dense ground cover (Fig. 2, Table 4, 23.91 ± 12.08) and less likely to colonize sites with deep leaf litter (Fig. 2, Table 4, −17.75 ± 11.06). Northern Cardinals were less likely to abandon sites with dense winter shrub density (Fig. 2, Table 4, −2.3

TABLE 4. Number of parameters (k) Akaike's Information Criterion value (AIC), difference in AIC from the top ranked model (ΔAIC) and model weight (w_i) for models of summer occupancy (Ψ), and colonization (γ) and local extinction (ε) of resident shrub-nesting birds in Tuskegee National Forest, Alabama. Only models within <2ΔAIC are shown.

Northern Cardinal				
Cover-type	k	AIC	ΔAIC	w_i
Development	9	950.46	0.00	0.42
Development + Agriculture + Scrub	11	952.06	1.60	0.19
Vegetation				
Grass Layer Density	10	947.36	0.00	0.36
Shrub Density	10	947.40	0.03	0.36
Eastern Towhee				
Ψ				
Cover-type	k	AIC	ΔAIC	w_i
Floodplain	9	648.92	0.00	0.41
Hardwoods	9	648.93	0.01	0.41
Vegetation				
Ground Cover + Grass layer Density + Midstory Density + Basal Area	13	647.09	0.00	0.29
Basal Area	10	648.86	1.77	0.12
Null	9	648.92	1.83	0.12
γ				
Cover-type	k	AIC	ΔAIC	w_i
Hardwoods	14	643.20	0.00	0.49
Floodplain	14	644.95	1.75	0.21
Vegetation				
Ground Cover + Leaf Litter Depth	16	637.60	0.00	0.82
Cover-type				
Null	16	637.60	0.00	0.33
Vegetation				
Ground Cover + Grass layer Density + Midstory Density + Basal Area	20	629.04	0.00	0.88
Brown Thrasher				
γ				
Cover-type	k	AIC	ΔAIC	w_i
Successional Scrub (Other) + Agriculture	8	250.38	0.00	0.56
Carolina Wren				
Ψ				
Cover-type	k	AIC	ΔAIC	w_i
Floodplain	8	1011.44	0.00	0.60
Vegetation				
Null	8	1011.44	0.00	0.25
γ				
Cover-type	k	AIC	ΔAIC	w_i
Floodplain	9	1010.96	0.00	0.22
Natural Pine	9	1011.19	0.23	0.19

TABLE 4. Continued.

Null	8	1011.44	0.48	0.17
Vegetation				
Canopy Cover + Leaf Litter	11	1003.03	0.00	0.54
Canopy Cover	10	1004.05	1.02	0.32
Cover-type				
Null	11	1003.03	0.00	0.26
Vegetation				
Ground Cover + Grass layer Density + Midstory Density + Basal Area	15	990.79	0.00	0.97

$\pm$ 1.16) and winter ground cover (Fig. 2, Table 4, -1.93 ± 0.94).

DISCUSSION

Our results demonstrate that in habitats in the southeastern US, partially migratory shrub-nesting birds increased occupancy in winter and had higher rates of site turnover between summer and winter than non-migratory shrub-nesting birds. Further, all species showed patterns of differing habitat use between summer and winter and selected habitat at multiple scales. Occupancy of non-migratory Northern Cardinals and Carolina Wrens decreased or remained static between summer and winter, whereas occupancy of partially migratory Brown Thrashers and Eastern Towhees increased. The decreased occupancy of non-migratory species between summer and winter is likely because of high levels of emigration from areas with certain types of cover or vegetation structure within the national forest. For example, Northern Cardinals were less likely to abandon developed sites, and therefore may immigrate into surrounding developed areas after breeding. Although we did not track marked individuals, the observed increase in occupancy of Eastern Towhees and Brown Thrashers between summer and winter is likely because of an influx of migrants, highlighting the importance for managing habitat for wintering shrub-nesting birds.

Rates of turnover further highlight the contrasting site use by birds having different migratory strategies. Site turnover was much greater for partially migratory species. Therefore, within our study site, partially migratory species are more likely to use sites during winter that were not occupied during summer. The observed rates of turnover of partially migratory species are likely because of differences in habitat needs between the breeding and non-breeding periods, or perhaps seasonal changes in resource availability within our study site (e.g., Bilcke 1984, Morrison et al. 1986, Keller and Yahner 2007). A high rate of turnover indicates that sites managed for breeding habitat, or preserved because they contain breeding individuals, are not likely to be used by wintering Brown Thrashers or Eastern Towhees.

Although partially migratory species had higher rates of turnover, all species showed differing patterns of habitat use between summer and winter. For instance, Northern Cardinals and Brown Thrashers were too ubiquitous and too sparse, respectively, to be associated with any particular type of cover during the breeding season. Occupancy of Brown Thrashers was greater during winter and colonization was more likely within wildlife openings. Use of wildlife openings by Brown Thrashers is likely underappreciated because Brown Thrashers do not use these open spaces for breeding. For example, Johnson (2010) did not detect enough Brown Thrashers for analysis during breeding season surveys of wildlife openings within Alabama, and Schlossberg and King (2007) do not list wildlife openings as used by Brown Thrashers in the eastern US. Therefore, the propensity of Brown Thrashers within our study site to colonize wildlife openings during winter highlights the need for a multi-season approach to studies of wildlife-habitat relationships.

Certain aspects of vegetation structure were also associated with changes in habitat use between summer and winter, particularly mea-

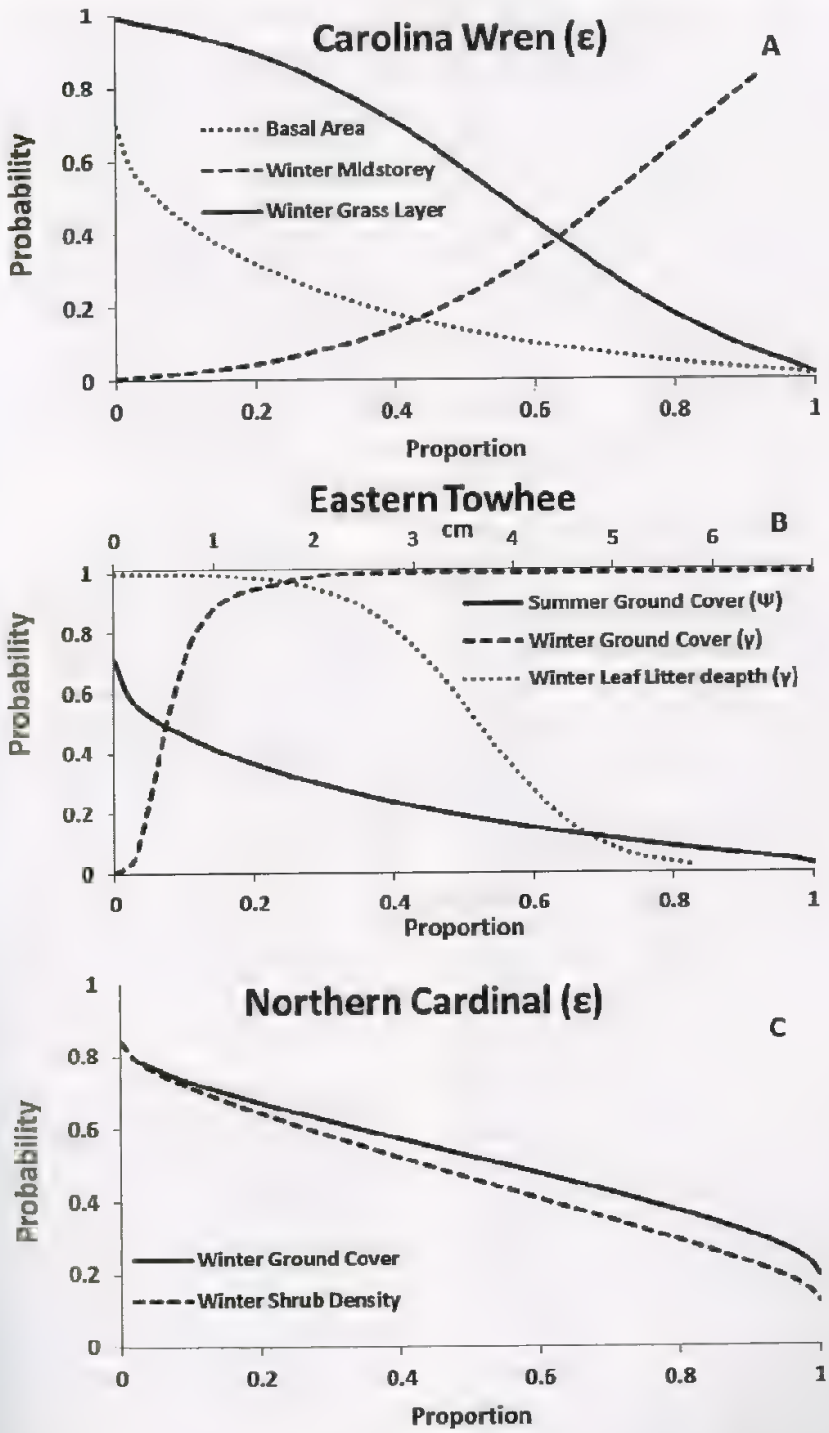

FIG. 2. A) Relationship between probability of local extinction (ε) between summer and winter of Carolina Wrens and aspects of vegetation structure at survey locations in Tuskegee National Forest, Alabama. B) Relationships of breeding occupancy (Ψ) and winter colonization (γ) and aspects of vegetation structure at survey locations in Tuskegee National Forest, Alabama. C) Relationship between probability of local extinction (ε) between summer and winter of Carolina Wrens and aspects of vegetation structure at survey locations in Tuskegee National Forest, Alabama.

sures of vegetation near the ground. Use of the ground layer by a bird community also changed seasonally in Pennsylvania with birds less likely to forage near the ground in the winter (Yahner 1987). Carolina Wrens and Northern Cardinals were less likely to leave sites with dense winter grass layer and ground cover, respectively. The pattern of differing habitat use between seasons is most striking for Eastern Towhees, which are less likely to occupy sites with dense ground cover during summer but more likely to colonize sites with dense ground cover during winter. Also, Eastern Towhees were less likely to colonize sites with a deep layer of leaf litter. The contrasting association of Eastern Towhees and ground cover during summer and winter may be a result of an increasing importance of plant material as food during winter or the need for leaf litter for nesting and foraging during summer (Greenlaw 1996), but more study is needed. Regardless of the mechanism, differing patterns of use of vegetation between seasons further highlight the pitfalls of basing management decisions on a single season.

Our results support not only the importance of multi-season approaches to the studies of shrub-nesting birds but also the importance of the multi-scale approaches suggested by numerous authors (e.g., Wiens et al. 1987, Wiens 1989, McClure et al. 2012). All four species were associated with certain cover-types. For example, use of habitat by Eastern Towhee seems characterized by avoidance of hardwood forests within our study site. Summer occupancy and probability of colonization by Eastern Towhee were negatively associated with floodplain forests and hardwood forests, respectively. Past studies showed that Eastern Towhees avoid hardwood forests (Rolek 2009) and prefer dry areas (Schlossberg and King 2007) and pine forests with scattered shrubby understory (Engstrom et al. 1984, Allen et al. 2006). Avoidance of hardwoods by Eastern Towhees within our site may be because of a preference for drier habitat, because hardwoods within our study site consist of floodplain and mesic slope forest. Therefore, Eastern Towhees first select sites that are not within hardwood forests, then selects sites with certain aspects of ground-level vegetation, depending on the season.

Our study underscores the importance of season and spatial scale when attempting to draw inference about the habitat associations of birds. All species analyzed in this study showed different habitat associations across seasons. For the management of such resident species, different types of cover or structures of vegetation may need to be maintained within a region. Information regarding vegetation structure and cover-type were important for all of our focal species suggesting that not only should certain types of cover be created and maintained but so too should certain structural aspects of vegetation within each cover-type. Species may also differ in use of habitat across their range (Collins 1983, Shy 1984, Graves 2002); this may hamper effective management actions if conservation strategies are based on research from other regions. Therefore, analysis of use of habitat at other sites across seasons and multiple scales should be a research priority.

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INFLUENCE OF HABITAT STRUCTURE AND FRUIT AVAILABILITY ON USE OF A NORTHEASTERN STOPOVER SITE BY FALL SONGBIRDS

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ABSTRACT.—Many studies have suggested that early successional habitats are important for fall migrant and resident birds. In light of this, we studied habitat relationships, preferred fruiting shrub species, and fruit consumption by birds in early successional habitats during the fall at Iroquois National Wildlife Refuge, Alabama, New York, USA. We used transects to count birds in 12 shrub and 6 early successional forest sites during 2008–2009, and collected data to construct habitat models. We examined frugivory using a paired open/enclosed fruit branch experiment and by analyzing fecal samples of birds captured in mist nets. More fall songbirds were detected in shrublands than in forests across the 2 years, although forests with well-developed understories also had high detection levels. Total bird abundance was positively related to fruiting species richness and negatively related to small woody stem (0.0–2.5 cm) abundance. Abundance of American Robins (*Turdus migratorius*) was positively related to total shrub cover and fruit abundance on common buckthorns (*Rhamnus cathartica*), and negatively related to small and large (2.5–8.0 cm) stem abundance. Abundance of Gray Catbirds (*Dumetella carolinensis*) was positively related to fruiting shrub species richness. Abundance of Song Sparrows (*Melospiza melodia*) was positively related to gray dogwood (*Cornus racemosa*) fruit abundance, and negatively related to small stem abundance and bella honeysuckle (*Lonicera* × *bella*) fruit abundance. Fecal analysis suggested that birds as a whole disproportionately consumed fruit species relative to availability, and consumed more bella honeysuckle and common buckthorn than gray dogwood. Fewer fruits remained on open branches than enclosed branches, suggesting birds actively consumed fruits at our sites. Our results suggest that fall migrant and resident songbirds as a whole benefit more from mature shrublands that contain a diversity of fruiting shrub species than from early successional forests. While these characteristics may benefit the suite of fall migrants and residents at our location, appropriate habitat management may differ for other locations or migratory species. *Received 17 April 2013. Accepted 23 August 2013.*

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Shrublands and early successional forests have declined in the Northeast as they have matured into secondary forests (Foster et al. 2002), which has lowered the available habitat for early successional habitat specialists (Litvaitis 1993). Recent research has suggested that many songbirds, both residents and migrants, use these habitats extensively during the fall (Rodewald and Brittingham 2004, Packett and Dunning 2009). Although previous studies have provided invaluable information on migrants, there are still many gaps in our understanding of their ecology and physiology, including what constitutes suitable stopover habitat for individual migrant songbird species and preferred fruit species.

Migratory songbirds spend up to 3 months of the year at stopover sites; therefore, having stopover habitat available in sufficient quantity and quality is important (Mehlman et al. 2005). These stopover sites are necessary for both resting and refueling (Parrish 2000, Bonter et al. 2007), as many small birds are unable to store enough fat to allow them to fly nonstop from breeding to wintering grounds. A number of studies point to fruits, particularly those in early successional shrublands, as an important source of energy for migrants during the fall (Parrish 1997, Smith et al. 2007, Smith and McWilliams 2010). While a diet containing both fruits and insects yields the best mass gains during stopover (Parrish 1997), insect abundance alone does not seem to be a good predictor of fall migrant habitat use in early successional canopy gaps (Champlin et al. 2009).

The main objective of this study was to determine which habitat characteristics migrant and resident songbirds select during the fall at Iroquois National Wildlife Refuge (INWR) in western New York, USA and model habitat use for the most common species. We used all birds encountered in the study, including species that used the site for migration stopover, as well as local breeders that used the habitat as staging ground for migration. We limited site selection to shrublands and early successional forests, as previous literature suggested these areas are important stopover habitats during migration (Suthers et al. 2000, Rodewald and Brittingham

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2004, Packett and Dunning 2009). Our secondary objectives were to determine fall frugivory levels among species, and preferred fruit species. Results of this study elucidate habitat relationships for fall migrants and residents in early successional habitats, and provide suggestions for managing these habitats to best support fall songbird populations.

METHODS

Site Description.—All sites were located at INWR in Alabama, New York, USA. (43° 6′ 44.6″ N, 78° 24′ 12.9″ W). INWR is approximately 4,400 ha and contains a variety of habitats including grasslands, shrublands, hardwood swamps, meadows, and freshwater marshes (USFWS 2010). We sampled 18 sites that ranged from 1.0–8.4 ha, including 12 shrublands and 6 early successional forest patches, from 1 September through 15 October in 2008–2009. Six of the 12 shrublands sites were located adjacent to the six early successional forest patches to allow us to limit effects of surrounding land cover when comparing early successional forest and shrubland use, while the remaining six shrublands were unpaired. We did not select sites randomly because of limited availability of early successional habitats at INWR and the need to sample specific habitat types. Shrublands were selected to include a wide range of habitat characteristics, from young and sparse to mature and dense, and contained the native gray dogwood (*Cornus racemosa*) and red osier dogwood (*Cornus sericea*), and the non-native bella honeysuckle (*Lonicera* × *bella*), common buckthorn (*Rhamnus cathartica*), and Russian olive (*Elaeagnus angustifolia*). Forests were primarily young, second growth stands and contained mostly green ash (*Fraxinus pennsylvanica*) and American elm (*Ulmus americana*), with lesser amounts of black walnut (*Juglans nigra*) and oaks (*Quercus* spp.). Land management histories for the forests are unknown; however, we found no evidence of logging, thinning, or planting, while the shrublands were managed as part of a rotational disturbance management regime to provide early successional habitat. The surrounding landscape was a mosaic of habitats, with forest surrounding many sites, although swamps or grasslands abutted some sites.

Habitat Characterization.—We used methods similar to those in James and Shugart (1970), with a few modifications, to characterize vegetation (Rodewald and Brittingham 2004). We placed four randomly stratified 5.0 m radius plots 12.0 m off alternating sides of bird count transects. Within each plot, we estimated both total and individual species shrub cover and counted shrub stems in the following categories: class one from 0.0–2.5 cm and class two from 2.5–8.0 cm diameter, each measured 10.0 cm above ground.

Within each 5.0-m radius habitat plot we calculated an index of fruit availability for each shrub species by multiplying the shrub cover by the estimated percent of the branches bearing fruit: Fruit Index = (Shrub Cover) * (Percent Branches with Fruit). We calculated total fruit availability index by summing all individual species indices: Total Fruit Index = Σ (Individual Species Indices). Although time constraints did not allow us to determine fruit density (number of fruits per m^3), we feel this index gives us a good estimate of relative fruit availability and is useful to make relative comparisons among fruiting shrub species. We also counted the number of shrub species bearing fruit per plot, as another indicator of fruit availability.

Bird Surveys

We used transect counts instead of mist nets to quantify bird abundance because transects require fewer resources, and previous studies have shown that transects and mist nets yield generally similar estimates of overall migrant abundance in early successional stopover habitats during the spring (Smith and Hatch 2008). While we did not perform our study in the same season as Smith and Hatch (2008), we feel the relationship between mist net and transect counts is still applicable (Mudrzynski 2010), given the high consistency of point counts and mist netting in assessing landbird abundance during fall and spring migrations (Wang and Finch 2002). Transects were located in the center of each patch and varied in length, according to the size of the patch. Densely wooded patches had 1–2 m wide lanes cut by brush hog or hand loppers prior to sampling to minimize disturbance to birds while walking transects. Each site was visited 7–8 times each year, with the exception of three sites that were visited up to 15 times each year to compare mist net and transect data (these data are not presented here). Single observers walked transects at ~1.0 km/hr between 0600–1000 EST when weather conditions did not hinder detectability (e.g., winds >24 km/hr and moderate to heavy

rain). Observers counted all birds in the habitat, recorded them to species and sex if possible, grouped unidentified birds into generic categories such as "bird", "sparrow", or "warbler", and estimated their distance and angle relative to the transect.

Fruit Consumption.—We used two methods to determine if fall birds consumed fruit in early successional habitats in 2009. First, we collected fecal samples from birds caught in mist nets by placing the birds in a paper bag for ~30 mins or until they produced a sample. Mist nets were located in two mature shrublands and one early successional forest and operated for the first 4 hrs after sunrise. We dissected fecal samples in the lab to find indicators of fruit consumption, including seeds or pulp in the feces as well as coloration (red, purple, etc.). We noted presence/absence of fruit for each fecal sample, rather than volume or mass, since we wanted to determine what fruit species the birds consumed, rather than determine total intake. Although coloration, regurgitation, or digestion may affect fruit detectability in the feces (Rosenberg and Cooper 1990), this was the best method for determining frugivory levels, given available resources and time. While we could not determine if fruits in fecal samples were consumed at our study sites, rapid gut passage times for fruits consumed by birds make it likely that fruits at least were consumed nearby (Herrera 1984, Karasov and Levey 1990). Second, we used an experimental field approach to determine if birds consumed fruits from shrubs (Smith et al. 2007). We counted fruits on two branches per individual shrub ($n = 5$ per species per patch), once per week throughout the fall of 2009 to determine if fruit consumption occurred; one branch served as a control, and the other was enclosed with a fine clear mesh to prevent access by birds. We performed this experiment for bella honeysuckle in three shrublands and two early successional forest sites ($n = 25$ paired branches) and in two shrublands for gray dogwood ($n = 10$ paired branches). Pairing branches in this manner allowed us to determine the amount of fruit lost from the shrub beyond that because of senescence. Additionally, we counted fruits during paired late evening/early morning counts to determine if small nocturnal mammals consumed fruits.

Statistical Analysis.—We constructed habitat models using only data from shrub sites because we observed few birds in forest sites. Prior to modeling, we standardized predictor variables (Z-score) to remove unit effects and then examined them in a correlation matrix to remove highly correlated variables ($r > 0.70$) (Shaw 2003). Data that failed normality tests were transformed with either arcsine square root (proportion data) or $\log_{10}$ (count data) transformations to improve normality (Zar 1999). We used backwards model selection (Gjerdrum et al. 2005) with the generalized linear model (GLM) module in SPSS 17.0 to generate habitat models based on total bird abundance and abundance of Gray Catbirds (*Dumetella carolinensis*), American Robins (*Turdus migratorius*), and Song Sparrows (*Melospiza melodia*), the three species with the greatest number of detections. We selected best habitat models using second order Akaike's Information Criterion (AIC_c) and reported full models with a $\Delta AIC_c < 2.0$ (Anderson and Burnham 2002). Finally, we used Akaike weights to determine the likelihood of each model being the best model given the current dataset (Anderson and Burnham 2002). We analyzed transect data using the Wilcoxon ranked sum test for the six paired, adjacent shrublands/forests and the Mann-Whitney *U*-test to compare relative abundances of birds between all 12 shrublands and six forests (Zar 1999). We used the half-cosine model in Distance 6.0 to calculate detection probabilities for all birds observed in shrubland and forest patches to help understand, in a very general way, the relative use of these habitats (Thomas et al. 2010). While grouping species together is not ideal because of differences in bird morphology and behavior, small sample sizes required us to group species to calculate a detection probability for forest birds. We did not correct individual species abundances for detection probability in the habitat modeling procedure, because we modeled species separately, did not analyze the two distinct habitat types together, and had low sample sizes.

We used the Wilcoxon ranked sum test in SPSS 17.0 to test the hypothesis that open branches lost fruit at a significantly faster rate than netted branches for bella honeysuckle, gray dogwood, and both species combined. We choose this non-parametric test because our data did not meet the assumptions for the parametric repeated measures ANOVA used in similar fruit removal studies (e.g., Smith et al. 2007). All five branches/treatment/species/patch were averaged together for each date, resulting in seven date pairs for each of the three analyses. We analyzed fecal data

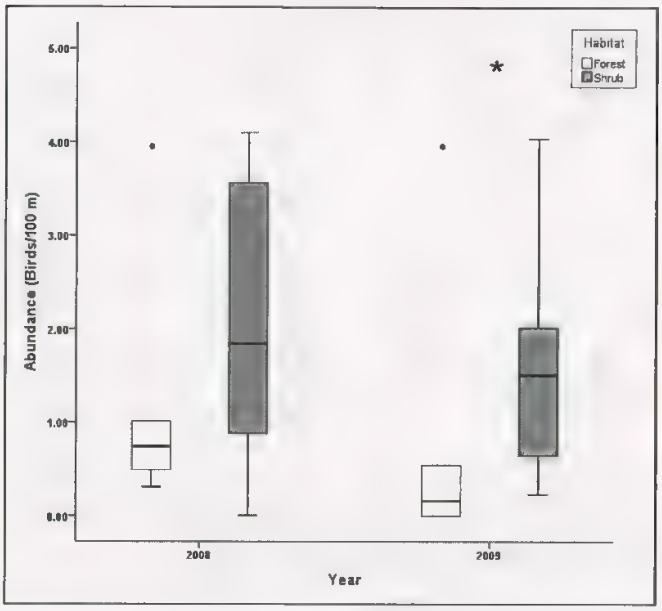

FIG. 1. Boxplot of transect bird abundance for all forest and shrubland sites in 2008–2009. The solid line, box, and whiskers represent the median, interquartile ranges, and minimum/maximum values, respectively. Site 10F (closed circle) was an outlier from the normal range of forest bird abundance in both years. Asterisk denotes a significant difference at the $P = 0.05$ level.

with a non-parametric χ^2 goodness-of-fit test to see if migrants consumed various fruit species disproportionately relative to fruit availability estimates.

RESULTS

Habitat Use.—We walked 291 transects during the study, including 133 in 2008 and 158 in 2009. Gray Catbirds, American Robins, and Song Sparrows were the most common species observed, collectively making up 43.6% and 50.2% of all birds counted in the transects in 2008 and 2009. Other common species included White-throated Sparrow (*Zonotrichia albicollis*), Common Yellowthroat (*Geothlypis trichas*), American Goldfinch (*Spinus tristis*), and Black-capped Chickadee (*Poecile atricapillus*). We were unable to identify 15.1% of the birds to species and therefore classified 3.3%, 11.5%, and 0.2% of the detections as "bird", "sparrow", and "warbler", respectively. While we tended to record more birds in 2008 than 2009, detections did not differ significantly between years for shrub sites (Wilcoxon: $Z = -1.490$, $P = 0.136$). Between-year differences approached significance for forest sites (Wilcoxon: $Z = -1.826$, $P = 0.068$), and for shrub and forest sites combined (Wilcoxon: $Z = -1.862$, $P = 0.063$), with slightly more bird detections in 2008 than 2009. There was no significant difference in bird detections between shrub and forest sites in 2008 (Mann-Whitney: $U = 22.0$, $P = 0.213$); however, more birds were detected in shrub than forest sites in 2009 (Mann-Whitney: $U = 13.0$, $P = 0.032$) and when years were combined (Mann-Whitney: $U = 74.0$, $P = 0.019$) (Fig. 1). Forest site 10F had a well-developed understory with mature honeysuckle plants and we observed 3.95 birds/100 m each year, comparable to the highest performing shrub sites (Fig. 1). When looking at paired sites alone, there was no significant difference in bird detections between forest and shrub sites in 2008 (Wilcoxon: $Z = -0.524$, $P = 0.600$), 2009 (Wilcoxon: $Z = -0.734$, $P = 0.436$), or years combined (Wilcoxon: $Z = -0.941$, $P = 0.347$). Detection probabilities for all birds in shrubland and forest patches were 0.18 (95% CI = 0.17–0.20) and 1.00 (95% CI = 0.67–1.00), respectively.

The best habitat model for total bird abundance suggested that more birds were detected in areas with more fruit-bearing shrub species and fewer small shrubs; the second-best model included a negative relationship with patch area (Table 1). Both models included year as a factor. The best habitat model for American Robins suggested that

TABLE 1. Best habitat models ($\Delta AIC_c < 2$) for all bird species combined for shrubland data only. Variable definitions are found in the Appendix.

Total bird abundance habitat models					
Rank	AIC_c	ΔAIC_c	w_i	Variable	β
1	70.48	0.00	0.43	Year	0.743
				Stem1	−0.597
				#Fruit Spp	0.984
2	70.92	0.44	0.42	Year	0.719
				Stem1	−0.733
				Area	−0.371
				#Fruit Spp	0.838

detections increased with increasing total shrub cover, decreasing numbers of stem classes one and two, and increasing buckthorn fruit abundance (Table 2). The best habitat model for Gray Catbirds suggested that detections increased with greater fruiting species richness (Table 2). Habitat modeling for Song Sparrows yielded three closely ranked models that suggested detections increased with gray dogwood fruit abundance and decreased with increasing stem class one abundance and honeysuckle fruit abundance (Table 2). Year also was included in the model with the lowest AIC_c value.

Fruit Consumption.—Of the 93 fecal samples collected, 27.7% contained at least one fruit species, with 11.1% of the samples containing material from honeysuckle, 3.3% from dogwood, 15.5% from buckthorn, and 2.2% from more than one species (Fig. 2). Feces from six of the eight bird species sampled contained evidence of fruit, with Gray Catbird (88.8%), Cedar Waxwing (*Bombycilla cedrorum*) (55.5%), American Robin (50.0%), and White-throated Sparrow (19.0%) showing the highest levels of frugivory, while the American Goldfinch and Common Yellowthroat showed no evidence of frugivory. Birds consumed fruits at different rates relative to abundance ($\chi^2 = 12.920$, df = 2, $P = 0.002$), with fecal samples showing more evidence of honeysuckle and buckthorn consumption than gray dogwood consumption.

When analyzing bella honeysuckle and gray dogwood combined, open branches had a significantly lower proportion of fruits remaining than netted branches throughout the course of the fall (Wilcoxon: $Z = -2.201$, $P = 0.028$) (Fig. 3). Bella honeysuckle showed the same significant trend (Wilcoxon: $Z = -1.992$, $P = 0.046$) while gray dogwood showed no difference in the proportion of fruit remaining on the two branch treatments (Wilcoxon: $Z = -0.105$, $P = 0.917$). There was no difference in the proportion of fruit remaining between the late evening and early morning counts ($t = 1.034$, df = 29, $P = 0.310$), suggesting that small mammals did not play a role in fruit removal. In addition, there were no indications of white-tailed deer (*Odocoileus virginianus*) browse on fruiting branches.

DISCUSSION

Habitat.—Our findings showed that fall migrants and resident birds, as a whole, utilize mature shrubland habitat more than early successional forests at INWR. Although bird abundance

TABLE 2. Best shrubland habitat models ($\Delta AIC_c < 2$) for American Robins, Gray Catbirds, and Song Sparrows Variable definitions are found in the Appendix.

Species	Rank	AIC_c	ΔAIC_c	w_i	Variable	β
AMRO	1	133.61	0.00	0.32	Shrubcov	2.930
					Stem1	−2.439
					Stem2	−1.985
					BuckFruit	1.239
GRCA	1	94.56	0.00	0.20	Year	1.118
					# Fruit Spp	1.167
	2	95.07	0.52	0.19	# Fruit Spp	1.095
SOSP	1	95.62	0.00	0.22	Year	0.693
					Stem1	−0.999
					RedPanFruit	0.524
					HoneyFruit	−0.322
	2	95.73	0.11	0.22	RedPanFruit	0.375
	3	95.88	0.26	0.22	Stem1	−0.699
					RedPanFruit	0.532

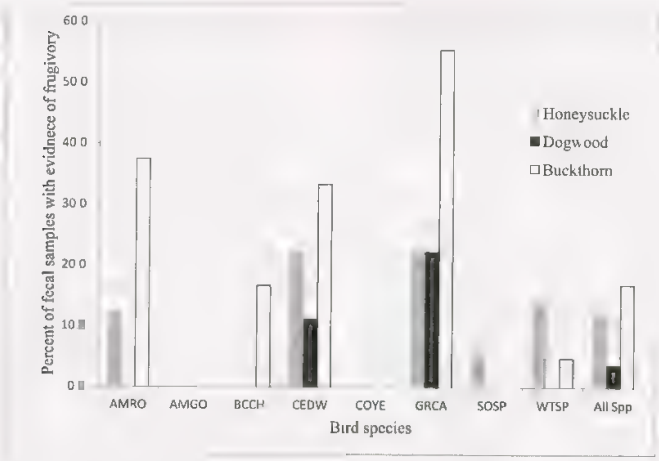

FIG. 2. Percent of fecal samples showing evidence of honeysuckle, dogwood, and buckthorn fruit consumption for American Robins (AMRO), American Goldfinches (AMGO), Black-capped Chickadees (BCCH), Cedar Waxwings (CEDW), Common Yellowthroats (COYE), Gray Catbirds (GRCA), Song Sparrows (SOSP), White-throated Sparrows (WTSP), and all species combined (data from patches 7S, 13S, and 13F). Some samples contained material from more than one fruit species; therefore, maximum evidence of frugivory is >100%.

data should be corrected for differences in detection probability prior to analyzing difference among habitats (Thomas et al. 2010), small sample sizes for forest detections did not allow us to correct our data for among-species differences in detection probabilities. However, two lines of evidence suggest that our uncorrected detection data depict an accurate, "real world" increase in use of shrubland habitats, relative to forest habitats, by fall songbirds at INWR. First, during our two-year study we detected very few birds in forest sites ($n = 72$), despite running 102 transects in forest habitats. Second, our calculation of overall detection probabilities for forest (1.0) and shrubland (0.18) birds, with their non-overlapping 95% confidence intervals—even if based on all detections—suggest that actual abundances in shrubland habitats were even greater than our uncorrected abundance data suggested. These uncorrected detection data

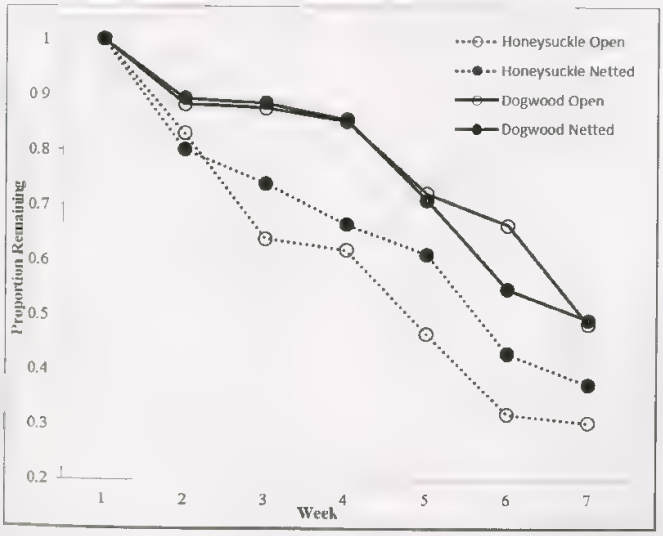

FIG. 3. Average proportion of bella honeysuckle and gray dogwood fruit remaining (untransformed data) for both netted and open branches during the 7-week study.

support the findings of previous studies in the Northeast, which show increased use of shrublands relative to forest habitat by songbirds during the fall (Suthers et al. 2000, Rodewald and Brittingham 2004, Smith and Hatch 2008, Packett and Dunning 2009).

Although transect detections were nearly two times greater in shrubland patches than forest patches, forest patch 10F (Fig. 1) did not follow this trend and each year yielded almost as many bird detections as some of the best shrublands. This forest patch had a more open canopy and well-developed understory (>60% shrub cover), which primarily consisted of large, fruit-bearing honeysuckle shrubs. Bird use of this forest patch suggested that fall birds might use some forest patches extensively if they possess a well-developed shrub layer.

The best habitat model for total bird abundance suggested that migrants and fall residents preferred mid-successional shrublands with a wide variety of fruiting shrub species. The negative relationship between total bird abundance with small stem (0.0–2.5 cm) abundance is the opposite of what Rodewald and Brittingham (2004) found; however, the discrepancy may be because of differences in our study sites. Our habitat models were based on younger successional sites, including young shrublands dominated by small-stemmed plants, while Rodewald and Brittingham (2004) used sites in Pennsylvania ranging from shrub/sapling forest to mature forest interior sites, which presumably had lower densities of small-stemmed shrubs. The negative relationship with small stems in our study, and positive relationship with small stems in Rodewald and Brittingham (2004), suggests that fall birds prefer a mid-successional shrubland with moderate densities of small stems. Rodewald and Brittingham (2004) also suggested that fruit abundance of early successional habitats is another important habitat selection factor for birds. Although in our study fruit abundance was not included as a variable in the best model for total bird abundance, fruit species richness was included as a positive predictor. Our results add to the literature demonstrating the importance of fruits to birds during the fall (Blake and Hoppes 1986, Parrish 1997, Suthers et al. 2000, Rodewald and Brittingham 2004).

Only one habitat model with a ΔAIC_c of <2 was generated for American Robins. The strongest predictor was a positive relationship with total shrub cover, suggesting that American Robins prefer well-developed, dense shrublands, although we found few in early successional forests. Klees (2008) found a negative relationship between shrub cover and abundance of American Robins during the breeding season at many of the same sites in INWR. This reversal in preference for shrub density within the same study sites suggests a shift in preferred habitat may occur between the breeding and fall migratory seasons, a finding reported elsewhere for fall migrants (Bowen et al. 2007). American Robins also preferred habitats that had fewer shrub stems, as shown by the negative relationships with both stem classes one and two, despite the positive relationship with shrub cover. These results suggest that American Robins prefer habitats with few, large and sprawling shrubs during the fall. The best model also included a significant positive relationship with buckthorn fruit abundance. This agrees with our fecal analysis results, which suggested that American Robins eat buckthorn at a disproportionate rate relative to the species' fruit abundance. Many bird species readily eat common buckthorn berries (Sherburne 1972, Whelan and Dilger 1992, Schmidt and Whelan 1999), though the potentially cathartic properties of buckthorn make our finding surprising (Sherburne 1972).

Gray Catbirds had two habitat models with a ΔAIC_c of <2; both included fruiting shrub species richness as a positive predictor of abundance. A similar variable, plant species richness, was positively correlated with habitat use by Gray Catbirds in western New York shrublands during the breeding season (Klees 2008). Although Smith et al. (2011) suggested that Gray Catbirds increase their use of forest habitat during migration, our data did not support this pattern. One forest patch did contain a few Gray Catbirds, but this site had a well-developed understory with mature honeysuckle shrubs.

The Song Sparrow was the only common species in our study that has declined significantly in New York State over the past 43 years (Sauer et al. 2011). The best habitat model for abundance of Song Sparrows included two negative predictors, stem class one abundance and honeysuckle fruit abundance, and one positive predictor, gray dogwood fruit abundance. A negative relationship between detections of Song Sparrows and stem class one might be related to the fact that the species typically occurred in patches with larger.

more developed shrubs. The remaining two variables showed that Song Sparrows occurred more in areas with higher levels of gray dogwood fruit and lower levels of honeysuckle fruit. Gray dogwood fruit abundance was also a positive predictor in the other two habitat models that had ΔAIC_c values < 2, which suggests this habitat variable is important for Song Sparrows in the fall.

Fruit.—The fruit removal experiment and fecal analysis were designed to answer two important questions: do birds consume fruit in shrublands and forests in the fall, and if so, which fruiting species do they prefer? While frugivory rates varied by species, approximately 28% of the fecal samples showed evidence of frugivory; these data suggested that birds were selective in their fruit consumption, mostly avoiding native dogwood and consuming more of the exotics like bella honeysuckle and common buckthorn. The three most frugivorous birds in our study were Gray Catbird, Cedar Waxwing, and American Robin; all showed evidence of frugivory in at least 50% of the fecal samples. Suthers et al. (2000) reported that Gray Catbirds and American Robins were among the most frugivorous species central in New Jersey during the fall, with fecal samples from each species consisting almost entirely of fruit, with no insect remains. The remaining common species in our study, American Goldfinch, Black-capped Chickadee, Common Yellowthroat, Song Sparrow, and White-throated Sparrow, had evidence of frugivory in <20% of the fecal samples (Fig. 2). Percentages of fecal samples with fruit residues were lower than for the same fall migrants in Rhode Island (Parrish 1997), although the percentages agree on the ranking of relative degree of frugivory among fall bird species.

The results of the fruit consumption experiment supported the fecal analysis, which suggested that most bird species we encountered eat fruit at fall stopover sites. The results also suggested that they consume the invasive bella honeysuckle, while avoiding the native gray dogwood, which explains the lack of dogwood fruit in fecal samples. The American Robin was the only thrush species encountered in our shrublands, despite the fact that *Catharus* thrushes are often the most common frugivores in shrublands, and they typically prefer native fruits (S. Smith, pers. comm.). Other thrush species may have avoided our sites because of the preponderance of invasive fruits, suggesting a species-specific response to invasive fruit preference or avoidance. Lafleur et al. (2007) reported that in choice trials, American Robins and European Starlings (*Sturnus vulgaris*) often preferred invasive fruits, though they speculated that the response is potentially species-specific for both the bird and fruit species. Our data do not agree with those of Drummond (2005), who used a similar branch exclosure method and reported that fall frugivores did not differ in their consumption of the invasive tartarian honeysuckle (*Lonicera tartarica*) and native silky dogwood (*Cornus amomum*), two species closely related to those used in our fruit removal experiment. While our data suggested a difference in consumption between native and exotic fruit species during the fall, a more comprehensive study using a wide range of fruit species is necessary before we can state that migrants preferentially consume invasive fruits. Although our data suggest that fruit consumption rates vary substantially among migrant species, the combined results of our fecal analysis and fruit exclosure study support the consensus that fruits are frequently consumed by many fall songbirds (Wheelwright 1986, Moss 1993, Suthers et al. 2000, Rodewald and Brittingham 2004, Smith et al. 2007, Packett and Dunning 2009).

Conservation and Management Implications.—Our results show that during the fall at INWR: (1) many bird species prefer shrublands to forests; (2) the presence of fruiting species may be an important factor in habitat selection for these birds; (3) many bird species consume fruits in shrublands. Given the apparent importance of shrublands and the fruiting species they contain for fall migrants and residents, the recent decline in early successional habitats in the Northeast should be viewed with concern (Litvaitis 1993, Foster et al. 2002). Moreover, early successional areas such as shrublands are highly susceptible to invasive shrub species such as bella honeysuckle and common buckthorn, as these species are often "r-strategists" (Hobbs and Huenneke 1992, Rejmanek and Richardson 1996, Lundgren et al. 2004). Our best habitat model for total bird abundance showed that fall birds tend to prefer habitats with increased fruiting shrub species richness; therefore, encroachment by exotic invasives could reduce the amount of available quality shrubland habitat by creating monocultures, which were present in some of the patches at INWR. However, fecal sample and fruit

removal data suggest that migrants use and may prefer the invasives bella honeysuckle and common buckthorn, relative to the native dogwood. Some sites at INWR dominated by exotic shrubs supported many birds during the fall. While we do not suggest encouraging exotic fruiting shrubs at places such as INWR, the cost of complete removal of exotic shrub species often makes this impractical (Westman 1990). Given the costs involved and the fact that these patches are providing some biological and ecological functions (Ewel and Putz 2004), a management plan whose goal is the complete removal of well-established exotic shrubs might not be the best use of available resources. Managers must balance the need for fall bird habitat with all other ecosystem needs and consider effects on the biological integrity, diversity, and environmental health before making this decision (USFWS 2009). Future studies should examine how well migrants perform (e.g., mass gained during stopover) by consuming invasive fruits to see if shrub habitats dominated by invasive, fruit-bearing species act as ecological traps (Schlaepfer et al. 2002).

The best habitat models differed among species, suggesting that no one management technique will provide the best habitat for all birds during fall. Habitat management targeting individual species may be difficult for places such as INWR because of limited resources; therefore, using the "All-Bird" habitat model to direct habitat management might be a good trade-off between habitat quality and resource use. Finally, some of our models differ from models produced by others during the breeding season, suggesting a habitat shift between seasons. This highlights the need for more research focusing on stopover habitat, which will allow for better management for songbirds during the fall; one of the Northeast priorities defined by Partners in Flight (Donovan et al. 2002).

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APPENDIX. Definition of habitat variables.

Variable name	Definition
Year	Year
ShrubCov	Total estimated shrub cover (%)
Stem1	Average class 1 stems (0−2.5 cm) per plot (Count)
Stem2	Average class 2 stems (2.5–8.0 cm) per plot (Count)
Honey1	Average class 1 honeysuckle stems (0–2.5 cm) per plot (Count)
Honey2	Average class 2 honeysuckle stems (2.5–8.0 cm) per plot (Count)
FruitIndex	Total fruit index (sum of individual fruit indicies)
HoneyFruit	Bella honeysuckle fruit index
BuckFruit	Common buckthorn fruit index
GrayDogFruit	Gray dogwood fruit index
RedOsierFruit	Red osier dogwood fruit index
OliveFruit	Russian olive fruit abundance
#FruitSpp	Fruiting shrub species richness
Area	Site area (ha)

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HOME RANGE AND HABITAT USE OF WINTERING VESPER SPARROWS IN GRASSLANDS OF THE CHIHUAHUAN DESERT IN MEXICO

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ABSTRACT.—Grassland birds are declining at an alarming rate and habitat limitation on the wintering grounds may play a major role in population declines. In an attempt to understand habitat needs and constraints of grassland bird species on their wintering grounds, we conducted the first-ever telemetry study to document the movements of a wintering grassland passerine bird in grasslands of the Chihuahuan Desert in northern Mexico. We attached radio-transmitters to 99 Vesper Sparrows in January of 2009 and 2010 and tracked them for up to 51 days. We estimated vegetation characteristics at foraging, roosting and random locations. We used kernel density estimators of the utilization distribution for each individual sparrow to estimate home range size. We found differences in average home range size between 2009 and 2010 (108.46 ± 36.43 ha and 30.91 ± 4.74 ha, respectively). Home ranges showed high levels of intraspecific overlap, with average pairwise overlap of 0.41, 0.70 and 0.79 among individuals at three study sites, as measured by the Bhattacharyya's affinity. Grasses and shrubs were shorter in foraging locations than in random sites within Vesper Sparrow core habitat, but we found no differences in grass cover and shrub cover. We suggest that movements of Vesper Sparrows are mostly limited to <1 km^2 during the winter and hypothesize that these movements are subject to constraints by food limitation and predation. *Received 9 March 2013. Accepted 15 August 2013.*

Key words: Chihuahuan Desert, grassland birds, habitat use, home range, radiotelemetry, *Pooecetes gramineus*, Vesper Sparrow.

Persistent declines in North American grassland bird populations represent one of the major wildlife conservation challenges of the 21st century. Grassland bird populations have been declining at the fastest rates among all bird guilds in North America since the 1960s (Samson and Knopf 1994, Sauer et al. 2011). The alteration of wintering habitat is a possible explanation for population declines in migratory bird species (Rappole and McDonald 1994); however, it has received less attention from researchers. Many grassland birds migrate south during the winter to the arid and semiarid grasslands and shrublands of the Chihuahuan Desert in northern Mexico (Peterson and Robbins 1999, Macias-Duarte et al. 2011). Habitat alteration in grasslands of the Chihuahuan Desert, such as the conversion of grasslands into farmland (Macías-Duarte et al. 2009), shrub encroachment (Van Auken 2000), and reduction in grass cover by overgrazing (Macías-Duarte et al. 2004) may be responsible for these population declines, but its impact on grassland bird populations has never been evaluated. Additionally, the winter ecology of many grassland birds wintering south of the United States remains largely unexplored which prevents the assessment of the long-term viability of grassland bird populations. Increasing our knowledge of the winter ecology of grassland birds is a research priority for addressing the conservation of these species (Vickery and Herkert 2001). Since grassland birds may be considered habitat specialists during the winter (Igl and Ballard 1999, Macías-Duarte et al. 2009), special attention must be paid to investigating mechanisms and strategies of habitat selection on their wintering grounds. In addition, the study of movement patterns and habitat selection during the winter could allow scientists to estimate species' area requirements and population capacity within existing grasslands.

The objective of this study was to contribute to filling gaps in our knowledge of the winter ecology of grassland birds by documenting movement patterns, home range size, and overlap and preferred habitat characteristics of a declining grassland bird species on its wintering grounds in Mexico using radio-telemetry. For this purpose, we studied the Vesper Sparrow (*Pooecetes gramineus*), populations of which have declined by 0.8% annually since 1966 (Sauer et al. 2011). Vesper Sparrows are one of the most abundant wintering grassland birds in the grasslands of the Chihuahuan Desert in northern Mexico (Jones and

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Cornely 2002, Macías-Duarte et al. 2009, Panjabi et al. 2010); they are relatively easily captured and large enough to carry a radio-transmitter that lasts up to 50 days.

METHODS

Study Area.—We conducted our research at the Reserva Ecológica El Uno, in the municipality of Janos, in the Mexican state of Chihuahua in the winters of 2009 and 2010. This property, owned and operated by The Nature Conservancy, spans 18,400 ha of grasslands and shrublands within a 526,482-ha federally protected biosphere reserve. Grasslands in the area are dominated by blue grama (*Bouteloua gracilis*), three-awn grasses (*Aristida* spp.), and tobosagrass (*Pleuraphis mutica*), with scattered woody plants such as honey mesquite (*Prosopis glandulosa*) and longleaf jointfir (*Ephedra trifurca*). We trapped Vesper Sparrows at three study sites on El Uno that were ~2 km apart: Corrales, Papalote, and Ratones. Corrales was added as study site in 2010. We chose these sites because they supported relatively high densities of Vesper Sparrows, particularly in 2010, when the species was scarce or absent from other available sites. Study sites had little or no to moderate grazing by American bison (*Bison bison*).

Bird Capture and Radio Telemetry.—We provide detailed information on bird capture and radio telemetry in Macías-Duarte and Panjabi (2013). In summary, we captured, banded, examined, and affixed radio transmitters to Vesper Sparrows from 6 January to 29 January in 2009 (9 banding dates) and from 7 January to 16 January in 2010 (7 banding dates). We placed Advanced Telemetry System® (ATS, Isanti, Minnesota, USA) transmitters (models A1015, A1025, and A1035) over the rump with a leg-loop harness made of beading elastic (Rappole and Tipton 1991). We tracked birds with four ATS radio receivers (model R2000) with headphones (David Clark model H10-00-4) and antennae (3-element folding Yagi). Two teams of two observers marked locations of each radio-tagged bird up to twice daily. We stopped tracking birds on 19 February 2009 and 25 February 2010.

Vegetation Surveys.—We provide detailed information on vegetation survey techniques in Macías-Duarte and Panjabi (2013). In general, we conducted vegetation surveys at each Vesper Sparrow telemetry location immediately after marking the location, and we returned to survey roost locations the next day. We conducted vegetation surveys within a 5-m radius circle around the telemetry location (10 m radius for roost locations), visually estimating average shrub and grass heights and percent cover of shrubs and grasses. Field technicians placed a 30-cm ruler vertically on the ground at each 5-m radius plot when estimating plot-level average grass height. Because this ruler was used as a visual reference point and 5-m radius plots were often clustered, occasionally field technicians did not use this ruler. Our visual estimation technique for grass and shrub cover produced estimates that were highly correlated to quantitative estimates of grass and shrub cover (Macías-Duarte and Panjabi 2013). To determine the habitat structure variables that influence Vesper Sparrow distribution, we collected the same vegetation parameters at 100 random locations within core use areas at each of the three study sites in 2010. We determined core habitat by plotting all bird telemetry locations in ArcMap™ 9.1 and used Hawth's Tools (Beyer 2004) Fixed Kernel Density Estimator (FKE) set at 90% probability of occurrence. We generated random points within 90% probability polygons using Hawth's Tools Random Point Generation. We assigned UTM coordinates to the random points and navigated to them with GPS units.

Data Analysis.—We estimated home range size using fixed kernel density estimators (KDE) of the utilization function (probability density function of sparrows' position in space) for each individual radio-tagged Vesper Sparrow (Seaman and Powell 1996) using package *adehabitat* (Calenge 2006) in program R v. 2.10.1 (R Development Core Team 2011). We used a bivariate Gaussian kernel and a reference bandwidth (Worton 1995). Seaman et al. (1999) recommend least squares cross validation (LSCV) to determine the level of smoothing or bandwidth of the kernel. However, frequent lack of convergence in LSCV estimates led us to use a reference bandwidth. We included individual Vesper Sparrows with ≥30 telemetry locations since this sample size is the minimum recommended by Seaman et al. (1999) for KDE of home range size. This procedure allowed us to estimate 41 home ranges. We also present KDEs for 74 Vesper Sparrows with ≥15 telemetry locations, enabling us to better capture variation in home range size; however, these estimates are of reduced precision and should be interpreted with caution.

We estimated home range overlap to make inferences on the degree of territoriality or association among individual Vesper Sparrows for 2010 data. We used Bhattacharyya's affinity (Fieberg and Kochanny 2005) as our working definition of overlap in home range (ω_{ij}) between any two individuals, which is defined as

$$\omega_{ij} = \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} \sqrt{f_i(x,y) f_j(x,y)}\, dx\, dy$$

where $f_i(x,y)$ and $f_j(x,y)$ are the utilization distributions for individuals i and j as determined by KDE, and x and y are easting and northing coordinates. This measure of overlap ranges from 0 (no overlap) to 1 (identical utilization distributions).

We attempted to determine which habitat features influenced the distribution of Vesper Sparrows by testing the null hypothesis that there was no difference between habitat structure at telemetry locations (known to be used by Vesper Sparrows) and random locations (unknown if used by Vesper Sparrows). We also tested whether vegetation characteristics at roosting and foraging locations differed, given that roosting locations are expected to meet high demands of protective cover from freezing night temperatures and predators. For both tests, we conducted statistical tests on the effects of a linear model and two-way ANOVA's with factor *LOCATION TYPE* (with levels foraging, roosting and random) and response variable vegetation (grass cover, grass height, shrub cover and shrub height). We included factor *SITE* (levels Corrales, Papalote, and Ratones) to account for variation introduced by differences between study sites. We conducted this analysis for the 2010 dataset only because we did not sample roost and random locations in 2009. We had a low sample size of roosting locations per individual (n = 1.1 locations per sparrow, range = 0–4) and we could not estimate differences between foraging and roosting locations at the individual level. Therefore, we conducted the analyses by pooling data from all individuals. We also tested whether vegetation characteristics at foraging locations differed between years using statistical tests on the effects of a linear model and two-way ANOVA both with factor *YEAR* (levels 2009 and 2010) and accounted for variation introduced by factor *SITE* (with levels Papalote and Ratones only). We set a significance level of $\alpha = 0.05$ for all statistical tests.

RESULTS

We recorded 522 telemetry locations for 33 individual Vesper Sparrows in 2009, but the number of telemetry locations per sparrow (n = 15.2 locations/bird, range = 1–32) was too low to obtain an accurate KDE of individual home ranges for most radio-tagged birds. In 2009 only three Vesper Sparrows had ≥30 telemetry locations; we estimated home ranges of 14.81, 42.07, and 205.20 ha for these three sparrows. The largest home range of 205.20 ha corresponded to a bird that moved once >2 km in opposite directions from its core home range. We considerably increased our sampling effort in 2010 with 2,712 telemetry locations for 68 Vesper Sparrows, 38 of which had ≥30 telemetry locations. We estimated an average home range size of 32.68 ± 6.39 ha for those 38 birds. When expanding our analyses to use data from Vesper Sparrows with ≥15 telemetry locations, average home range was 108.46 ± 36.43 ha (n = 20) and 30.91 ± 4.74 ha (n = 54) in 2009 and 2010, respectively (Fig. 1).

Vesper Sparrows showed high levels of overlap in their winter home ranges within study sites reflecting the common use of a single large central area (Fig. 2, for 2010 only). We estimated home range overlap of 0.7039 ± 0.0183 (range: 0.1444–0.9668) at Corrales, of 0.4841 ± 0.0295 (range: 0.0108–0.9717) at Ratones, and of 0.7943 ± 0.0119 (range: 0.3502–0.9826) at Papalote.

Vesper Sparrows used areas with shorter vegetation than what was available in their core habitat and showed no preference for percent ground cover (Table 1). Mean grass height and mean shrub height were significantly lower at telemetry locations than at random locations (P = 0.040 and $P < 0.001$, respectively). Comparisons between telemetry locations and random locations showed no statistical difference for grass (P = 0.92) or shrub cover (P = 0.108) accounting for the significant differences between study sites (two-way ANOVA $P < 0.001$ for all vegetation variables). In addition, grass height and grass cover at roost locations were significantly higher than those at foraging ($P < 0.001$ and P = 0.008, respectively) and random locations ($P < 0.001$ and P = 0.015, respectively, Table 1). However, we did not detect differences in mean shrub height and mean shrub cover between roosting and

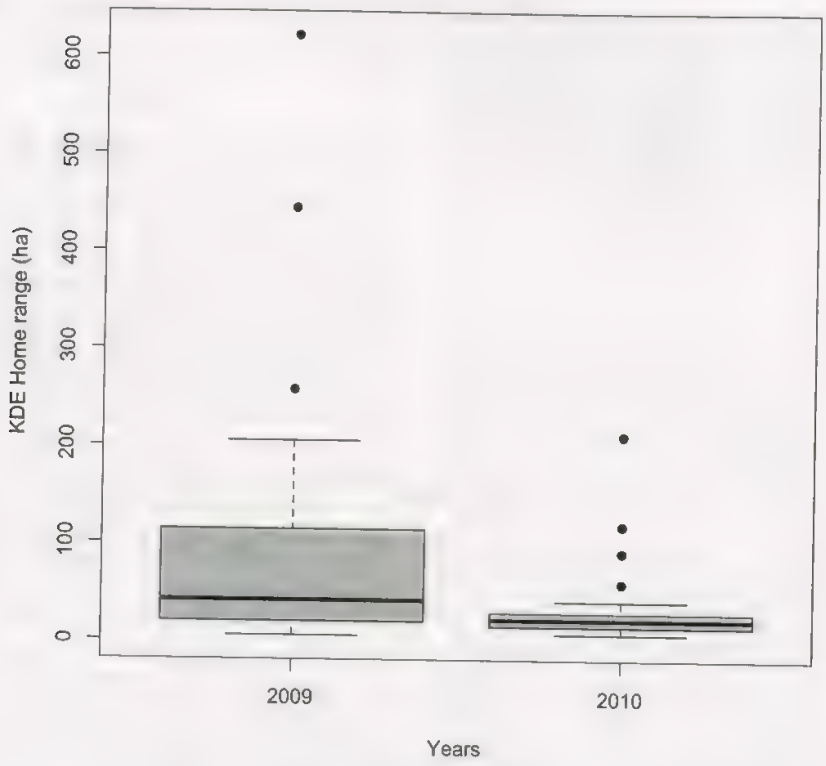

FIG. 1. Distribution of home range sizes for Vesper Sparrows with ≥15 telemetry locations in 2009 (n = 20) and 2010 (n = 54) in desert grasslands of Janos, Chihuahua, Mexico, as determined by 95% kernel density estimates (KDE). Boxplots represent the distribution of individuals' home range sizes in 2009 and 2010. Box height denotes the interquartile range (IQR) of home range size in each year. The horizontal black line is located at the median value of home range size. Upper and lower whiskers denote the minimum and maximum home range sizes not smaller and not larger than 1.5 times the IQR from the box, respectively, and black circles are home range size values beyond these limits.

foraging locations (P = 0.16 and P = 0.34, respectively) or random locations (P = 0.74 and P = 0. 90), after accounting for differences between study sites. We observed taller grasses at foraging sites for Vesper Sparrows during winter 2009 than during winter 2010 (Table 1). This pattern is probably the result of a wetter summer prior to winter 2009 (2008 summer precipitation = 397 mm) compared to that of winter 2010 (2009 summer precipitation = 123 mm, data collected in Casas Grandes, 70 km south).

DISCUSSION

Our results provide the first estimates of winter home range size for the Vesper Sparrow and suggest that most individuals (89%) remain within home ranges <1 km^2 (<100 ha) during the winter. In comparison, other grassland emberizids have smaller estimated mean winter home ranges of 9.1 ha for Savannah Sparrows (*Passerculus sandwichensis*) in the coastal marshes of south Texas (Ginter and Desmond 2005) and 0.3 ha for Henslow's Sparrows (*Ammodramus henslowii*) in the coastal longleaf pine savannas of Mississippi (Bechtoldt and Stouffer 2005). Previous estimates of breeding territory size of Vesper Sparrows vary from 0.29 to 8.19 ha (Jones and Cornely 2002), although breeding territory size and winter home range may not be comparable. Our results suggest Vesper Sparrows require a larger, fixed home range in winter, although there appears to be a high degree of home range overlap among individuals. This corroborates the conclusions of Gordon (2000) who stated that Vesper Sparrows tended to remain within fixed winter home ranges in desert grasslands of southeastern Arizona; however, this author did not provide any estimate of home range size. As Gordon (2000) noted, fixed winter home ranges may be an adaptive strategy in desert ecosystems when there is consistency in spatial precipitation patterns and food supply by allowing birds to conserve energy

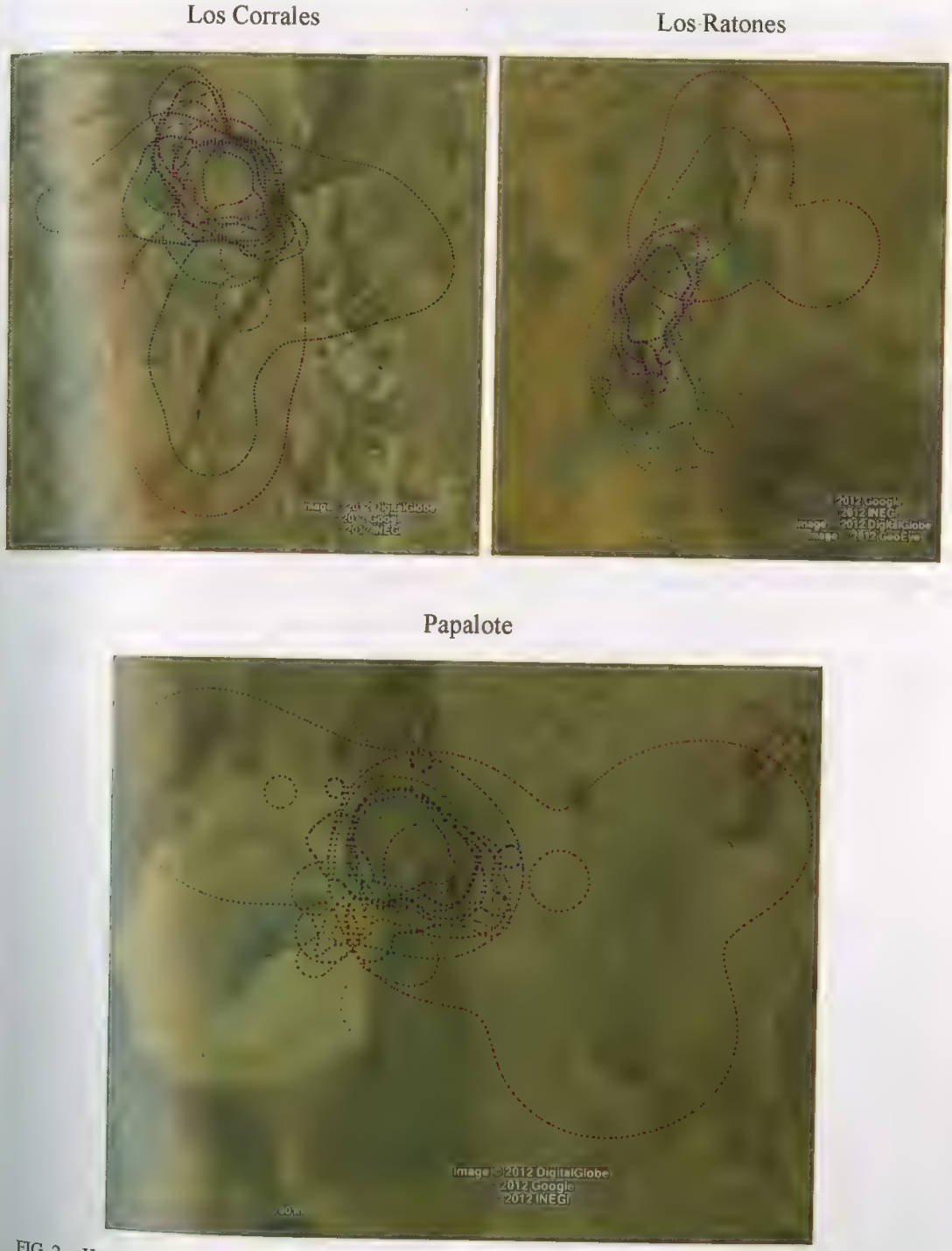

FIG. 2. Home range boundaries of individual Vesper Sparrows with ≥15 telemetry locations at study sites Corrales (n = 19), Ratones (n = 15), and Papalote (n = 20) in desert grasslands of Janos, Chihuahua, Mexico, in 2010, as determined by 95% kernel density estimates (KDE). Each color indicates an individual sparrow.

TABLE 1. Mean vegetation characteristics at foraging and roosting locations of radio-tagged Vesper Sparrows and at random sites within sparrow home ranges in desert grasslands of Chihuahua, Mexico during the winters of 2009 and 2010 at study sites in Papalote, Corrales, and Ratones. Symbols *, and ^{NS} denote *P*-values of <0.05, and >0.05, respectively, for testing the pairwise difference of means in habitat characteristics between foraging locations in 2010 and 2009 (two-way ANOVA with factors *SITE* and *YEAR*) and roost and random locations in 2010 (test on effects of a linear model with factors *SITE* and *LOCATION TYPE*). All vegetation characteristics differed significantly between sites in both years (two-way ANOVAs, $P < 0.001$). Boldface numbers denote a significant difference ($P < 0.05$) in the mean of habitat characteristics between roosting and random locations.

		2009	2010		
Vegetation parameter	Site	Foraging	Foraging	Roosting	Random
Grass height (cm)	All sites	30.4*	22.3	**29.8***	**23.8***
	Corrales	—	20.7	28.8	19.6
	Papalote	29.1	19.1	30.4	24.2
	Ratones	31.0	25.9	29.0	27.5
Grass cover (%)	All sites	53.0^{NS}	46.0	**54.5***	**44.9**^{NS}
	Corrales	—	29.3	43.3	27.1
	Papalote	59.1	43.6	57.0	42.1
	Ratones	47.6	61.2	58.0	65.3
Shrub height (m)	All sites	1.11*	0.78	0.59^{NS}	0.61*
	Corrales	—	0.75	0.88	0.76
	Papalote	1.09	0.59	0.39	0.40
	Ratones	1.09	0.93	0.76	0.67
Shrub cover (%)	All sites	21.4**	9.0	6.1^{NS}	7.9^{NS}
	Corrales	—	12.8	16.5	14.5
	Ratones	23.8	9.3	5.4	4.0
	Papalote	18.6	4.5	2.6	4.0

otherwise devoted to nomadic movements. Yet, we cannot rule out the possibility that more mobile and nomadic individuals exist in our study population, as documented in other desert granivorous bird assemblages (Blendinger and Ojeda 2001). As 25% of our live birds escaped detection before day 23 post transmitter deployment (estimated battery life for the smaller radio-transmitter), some segment of the wintering population may have abandoned the study area to seek new foraging patches out of our range. However, we believe that most birds were lost because of radio-transmitter battery failure. We directly observed a radio-tagged bird in the field emitting no signal before the expected battery life had expired.

Grassland sparrows wintering in the Chihuahuan Desert have a specialized diet of grass and herbaceous seeds (Desmond et al. 2008), and the magnitude of grass seed production is directly related to summer rains in desert ecosystems (Pol et al. 2010). Thus, food limitation may become a major ecological process for grassland birds in southwestern desert grasslands in years of low seed production (Pulliam and Dunning 1987). Therefore, we found it puzzling that home ranges were larger in 2009 when grass conditions and possibly seed food resources were better, and thus the need for exploratory foraging movements was lower than in 2010.

Predation is a major ecological process driving the response of bird species to habitat structure in desert grasslands of North America (Lima and Valone 1991). Given that winter passerine abundance in grasslands of the Chihuahuan Desert is related to summer precipitation, winter predation pressure may be lower following wetter summers because of the higher availability of alternative bird prey (Dunning and Brown 1982, Macías-Duarte et al. 2009). In addition, predation pressure may be lessened by the increased cover provided by greater grass vegetation volume in wetter years. Therefore, a potential explanation for larger home ranges in 2009 is that predation pressure restricted the movements of Vesper Sparrows in 2010. It is likely that winter home ranges of Vesper Sparrows are shaped by an interaction between food limitation and predation.

Grasses and shrubs were significantly shorter in telemetry locations than in random locations (2010 dataset only), but we found no difference in grass cover and shrub cover. The estimated significant difference in grass height (1.8 cm after

accounting for differences between study sites) seems relatively small to be biologically meaningful. Because we trapped birds in areas of high relative abundance (and possibly in preferred habitat), we may have failed to detect variability in habitat structure and thus larger differences between telemetry and random locations especially in areas where sparrows were less abundant. Yet, a decrease in grass height of 1.8 cm decreases average survival time of Vesper Sparrows by almost 30% ($e^{(0.1408 \cdot 1.8cm)}$, Macías-Duarte and Panjabi 2013). Given that use of areas with shorter grasses and shrubs decreases survival probability (Macías Duarte and Panjabi 2013), the preference for shorter vegetation suggests a trade-off between predation risk and food availability; Vesper Sparrows may forage more efficiently in areas with shorter grasses (Whittingham and Devereux 2008) and shrubs but may be more easily detected by predators and less able to avoid a predatory attack.

The importance of shrubs to Vesper Sparrows has been widely documented: abundance of Vesper Sparrows increases with experimental addition of woody elements in open grasslands (Lima and Valone 1991) and they tend to forage <4 m away from shrubs, using shrubs to avoid predators (Pulliam and Mills 1977). Although shrubs are likely an important component of winter habitat for Vesper Sparrows, we may have failed to detect the influence of shrub cover because we focused trapping efforts in areas with relatively high densities of tall shrubs. Further, the influence of shrub distribution on habitat selection and home range patterns may only be evident at larger spatial scales. For example, home ranges of Vesper Sparrows closely followed the distribution of shrubs (e.g., Ratones in Fig. 2).

Vegetation characteristics at roosting locations should provide thermal refuge from freezing night temperatures (mean winter daily minimum temperature as low as −0.1 °C in our study area) as well as cover from predators, and likely differ from foraging areas. Our data support this assertion for Vesper Sparrows wintering in the Chihuahuan Desert; roosting sites had significantly higher grass and shrub cover than foraging areas. Similarly, foraging and roosting locations for Savannah Sparrows differed in the amount of bare ground and total cover (Ginter and Desmond 2005).

Our research provides the first estimate of home range size for a declining migratory bird species on its wintering grounds in the Chihuahuan Desert, where a large portion of North American grassland birds overwinter. Our estimates of home range size, overlap, and habitat characteristics can be applied to the conservation of Vesper Sparrows. More specifically, this data could be used to estimate the winter carrying capacity of grasslands in the Chihuahuan Desert for this species. However at this time, we do not have precise estimates of the extent of available habitat for Vesper Sparrows. Additionally, relationships between winter home range and summer precipitation (via grassland vegetation conditions) must be further explored in the context of increased aridity projected for the Chihuahuan Desert region as a result of global climate change (Seager et al. 2007).

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MULTISCALE NEST SITE SELECTION BY BURROWING OWLS IN WESTERN SOUTH DAKOTA

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ABSTRACT.—Grassland bird species frequently respond to habitat characteristics at multiple spatial scales when selecting nest sites. The Western Burrowing Owl (*Athene cunicularia hypugaea*) is a grassland bird species of conservation concern across much of its range, but most studies of its habitat needs have been restricted to relatively small geographical areas and have not integrated multiple spatial scales. Our study examined habitat characteristics at three spatial scales—local (near the burrow), colony, and landscape—across western South Dakota. We searched for Burrowing Owls in 107 prairie dog colonies from May to August 2011. We located nest burrows in owl-occupied colonies, and we randomly selected non-nest burrows in colonies that were not occupied by owls for comparison. We collected data for local habitat variables in the field. Ground truthing and aerial imagery were used to calculate colony and landscape variables. We used logistic regression to identify variables that impacted nest site selection. Variables at multiple scales were important, with percent tree cover within 800 m of the burrow and visual obstruction at the burrow having the greatest effect on nest site selection. Burrowing Owls in western South Dakota were most likely to nest in landscapes with little tree cover, perhaps to avoid large avian predators associated with trees. At the local scale, Burrowing Owls were most likely to nest in regions of prairie dog colonies with relatively low visual obstruction. Burrowing Owls may benefit from prairie dogs maintaining vegetation at a short height, which allows the owls to easily detect prey and predators. Maintaining active prairie dog colonies in open landscapes across western South Dakota and preventing the establishment of trees near prairie dog colonies is necessary to ensure preferred breeding habitat remains for Burrowing Owls. *Received 17 January 2013. Accepted 14 June 2013.*

Key words: black-tailed prairie dog, Burrowing Owl, mixed grass prairie, multiscale habitat selection, nesting habitat, South Dakota, western South Dakota.

The Western Burrowing Owl (*Athene cunicularia hypugaea*, hereafter 'Burrowing Owl') is a species of concern throughout much of its North American range, as many populations have shown signs of decline (Johnsgard 2002, Klute et al. 2003, Poulin et al. 2011, Sauer et al. 2011). In South Dakota, the Burrowing Owl has been identified as a Species of Greatest Conservation Need in the South Dakota Wildlife Action Plan (South Dakota Department of Game, Fish, and Parks 2006) and a Level I priority species in the South Dakota All Bird Conservation Plan (Bakker 2005).

Burrowing Owls breed primarily in the western half of South Dakota (Peterson 1995, Tallman et al. 2002). Burrowing Owls nest underground, rarely, if ever, creating their own nest burrows but instead using burrows created by semi-fossorial mammals (Johnsgard 2002, Poulin et al. 2011). In South Dakota, Burrowing Owls are closely associated with colonies of black-tailed prairie dogs (*Cynomys ludovicianus*, hereafter 'prairie dogs'). A strong affinity for prairie dog colonies is typical of Burrowing Owls in regions where prairie dogs are present. Other researchers have surveyed for Burrowing Owls in prairie dog colonies and surrounding uncolonized grasslands and found that most or all Burrowing Owls nested in prairie dog colonies (Butts and Lewis 1982, Thompson 1984, Agnew et al. 1986, Plumpton and Lutz 1993, VerCauteren et al. 2001, Conway and Simon 2003, Winter et al. 2003, Tipton et al. 2008). To our knowledge, only one study of Burrowing Owls nesting within the geographic range of prairie dogs did not find prairie dog colonies to be the predominant source of nest sites (Korfanta et al. 2001).

Loss of prairie dog colonies to poisoning, land conversion, and sylvatic plague (a disease caused by the bacterium *Yersinia pestis*) has been linked to declining populations of Burrowing Owls (Desmond et al. 2000, Holroyd et al. 2001). However, because not all prairie dog colonies are occupied by Burrowing Owls, the loss of potential nest sites cannot completely account for population declines. Orth and Kennedy (2001) commented that the decreasing availability of potential nest sites was probably not a limiting factor for the

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population of Burrowing Owls in eastern Colorado; many prairie dog colonies were not occupied by owls, implying that competition was not particularly high for nest sites.

Much research has been conducted on habitat use by Burrowing Owls in different regions. Most quantitative studies of their habitat have been conducted at the 'local' or 'microhabitat' scale, examining habitat characteristics immediately around nest burrows and comparing them with those of non-nest burrows. Results have been inconsistent among studies, but some habitat characteristics found to differ between nest and non-nest burrows include vegetation composition (Thompson 1984, MacCracken et al. 1985), vegetation structure (Green and Anthony 1989, Plumpton and Lutz 1993), and density or proximity of prairie dog burrows (Plumpton and Lutz 1993, Desmond et al. 2000, Poulin et al. 2005).

Studies of larger-scale habitat characteristics selected by Burrowing Owls have been less common. Some studies have compared the sizes of prairie dog colonies occupied by Burrowing Owls to colonies that were not occupied by owls, but results were mixed. Griebel and Savidge (2007) found that owl-occupied colonies were larger; in contrast, Plumpton and Lutz (1993), Orth and Kennedy (2001), and Restani et al. (2001) found no size difference between occupied and unoccupied colonies. Few studies have examined landscape-scale habitat characteristics. Orth and Kennedy (2001) found that Burrowing Owls in northeastern Colorado were more likely to occupy prairie dog colonies in patchy landscapes than in unfragmented shortgrass landscapes. In western North Dakota, Restani et al. (2008) found that the number of pairs of Burrowing Owls in a prairie dog colony was positively associated with cover of crops, crested wheatgrass (*Agropyron cristatum*), and prairie dog colonies in the surrounding landscape.

Models that incorporate variables from multiple scales are frequently better predictors of grassland bird occurrence and density than single-scale models (Bakker et al. 2002; Fletcher and Koford 2002; Cunningham and Johnson 2006; Winter et al. 2006a, b; Renfrew and Ribic 2008). A literature search revealed only two nesting studies on Burrowing Owls that incorporated local-, colony-, and landscape-level variables—one on the Thunder Basin National Grassland in northeastern Wyoming (Lantz et al. 2007) and the other on the privately-owned Bad River Ranches in central South Dakota (Bly 2008). Results of both studies supported a multiscale approach to modeling habitat selection by Burrowing Owls. Lantz et al. (2007) found that models incorporating local (burrow length, number of burrows, and percent shrub cover), colony (percent prairie dog activity), and landscape (distance to water) variables were the best predictors of presence of Burrowing Owls' nest burrows. Bly (2008) found that prairie dog colony size alone was the best predictor of nest density, but a model incorporating landscape variables (isolation from other colonies and colony habitat type, i.e., upland or lowland) along with colony size was the best predictor of Burrowing Owls' breeding productivity.

Conserving prime habitat for Burrowing Owls requires a better understanding of habitat characteristics that make some potential nest sites more suitable than others. Our objectives were to determine local, colony, and landscape habitat variables that are useful for segregating prairie dog colonies that contain nests of Burrowing Owls from colonies that do not contain nests and to determine the scale/s at which Burrowing Owls respond to habitat changes across a large geographic area. This information is needed by managers seeking to conserve suitable habitat for Burrowing Owls so that a stable population can be maintained. Our study followed the multiscale approach of Lantz et al. (2007) and Bly (2008), but our study area was larger and more ecologically diverse, with many land uses represented. Unlike the previous multiscale studies, our study incorporated land use variables, because we hypothesized that conversion of grasslands to croplands and the incorporation of woody vegetation into the landscape has an effect on Burrowing Owls' nest site selection. Although several authors have commented that Burrowing Owls seem to prefer landscapes with few or no trees (Wedgwood 1976, Clayton and Schmutz 1999, Poulin et al. 2011), only Stevens et al. (2011) quantified tree cover in a Burrowing Owl habitat study.

METHODS

Study Area.—South Dakota is divided approximately in half by the Missouri River. We conducted our study in the western half (Fig. 1), with the exception of the forested Black Hills region, which does not contain habitat for Burrowing Owls (Tallman et al. 2002). Regional

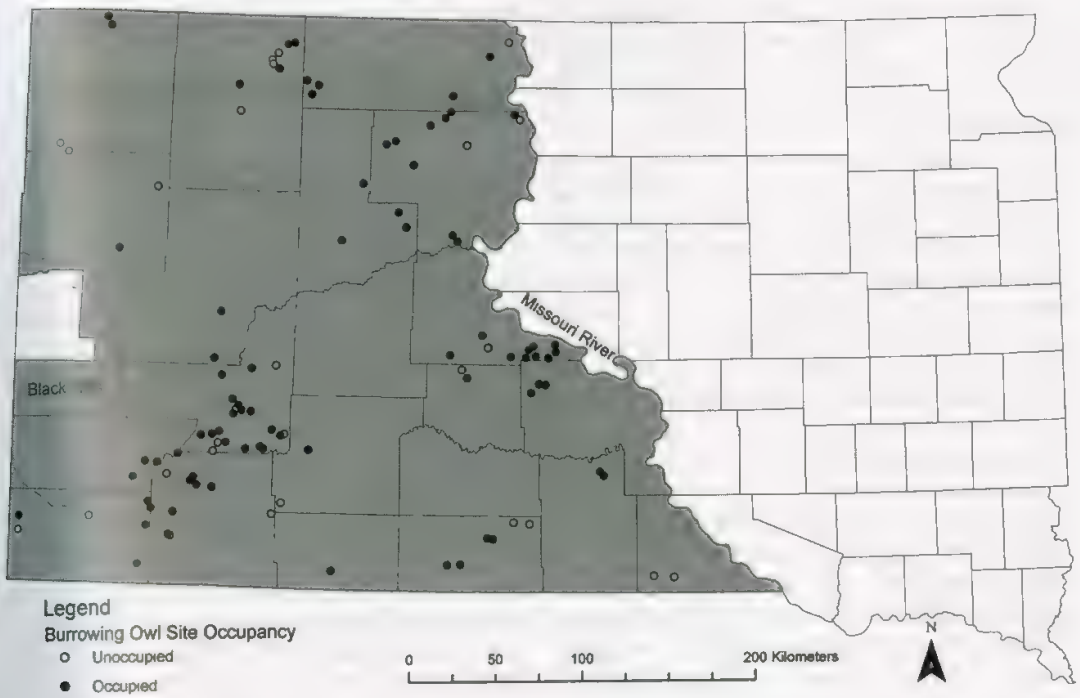

FIG. 1. Map of South Dakota with the study area counties highlighted in gray and prairie dog colonies surveyed for Burrowing Owls represented by black and white circles. Occupied colonies (n = 80) contained at least one Burrowing Owl nest, and unoccupied colonies (n = 27) contained no nests.

climate is characterized by cold, dry winters and hot summers, with much of the annual precipitation coming in summer thunderstorms. Precipitation generally decreases from east to west across the study area (High Plains Regional Climate Center 2012). Topography consists mostly of flat to rolling plains dissected by drainages. However, badlands formations are abundant in parts of southwestern South Dakota, and buttes and rocky outcrops can be found locally across most of the study area.

Dominant vegetation within prairie dog colonies varies with factors such as soil type, precipitation, prairie dog density, and livestock grazing pressure. Western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), buffalograss (*Bouteloua dactyloides*), purple threeawn (*Aristida purpurea*), and sedges (*Carex* spp.) were commonly encountered native graminoid species in our study area. Non-native crested wheatgrass has been commonly planted as a forage species and in some areas was the dominant grass species. Another introduced species, cheatgrass (*Bromus tectorum*), was an invasive grass through much of the study area. Common native forbs within and near prairie dog colonies included wooly plantain (*Plantago patagonica*), scarlet globemallow (*Sphaeralcea coccinea*), prickly pear (*Opuntia* spp.), snow on the mountain (*Euphorbia marginata*), western yarrow (*Achillea millefolium* L. var *occidentalis*), fetid marigold (*Dyssodia papposa*), and longbract spiderwort (*Tradescantia bracteata*). Commonly encountered exotic forb species included nodding plumeless thistle (*Carduus nutans*), field bindweed (*Convolvulus arvensis*), common mullein (*Verbascum thapsus*), and sweetclover (*Melilotus* spp.). Sagebrush (*Artemisia* spp., primarily *Artemisia tridentata*) was a major vegetative component in a few areas, but it was usually clipped to the ground by prairie dogs within the boundaries of colonies. Trees encountered throughout the study area were generally species associated with riparian areas such as plains cottonwood (*Populus deltoides*), willow (*Salix* spp.), boxelder (*Acer negundo*), and green ash (*Fraxinus pennsylvanica*) or species planted in shelter belts such as cottonwood, eastern red cedar (*Juniperus virginiana*), and the introduced Russian olive (*Elaeagnus angustifolia*). Eastern red cedar was also a

frequent and increasing species in drainages in some areas. Ponderosa pine (*Pinus ponderosa*) was a locally common species near the Black Hills in the west and the Pine Ridge Escarpment in the southwest.

Private, state, federal, and tribal lands were well represented in the study area. Human population is sparse, and ranching is the most common land use. Most prairie dog colonies were located on pasture land used for grazing by livestock. Prairie dog populations were periodically controlled throughout most of the study area. Many of the colonies surveyed during this study had been poisoned within the previous 1–5 years, and many were also subjected to recreational prairie dog shooting according to local landowners and managers.

Haying of forage crops such as alfalfa (*Medicago sativa*) and some native and introduced grasses was also common. Row crop and/or small grain agriculture was generally restricted to areas with topography suitable for cultivation but could be found in all counties in the study area. Common crops were common wheat (*Triticum aestivum*), corn (*Zea mays*), and soybeans (*Glycine max*).

Local (Nest Site) Habitat Data Collection.—From 25 May 2011 to 9 August 2011, we searched for nest sites of Burrowing Owls in 107 prairie dog colonies selected from across the study area (Fig. 1). Selection was pseudo-random; we divided each county into 'clusters' of prairie dog colonies based on geography and colony density and then randomly selected 1–5 colonies from each cluster in proportion to the number of colonies found in the region. If we could not obtain permission to access a randomly selected colony, we selected the nearest colony that we could access. All selected colonies were ≥1,600 m apart to avoid pseudoreplication of landscape variables. Colonies that lacked prairie dogs (because of poisoning or sylvatic plague outbreaks) were rejected from our sample. We spent a minimum of 20 mins systematically surveying each colony with binoculars and/or a spotting scope. In larger colonies, we spent several hours surveying from multiple vantage points to ensure complete coverage. We noted the locations of all Burrowing Owls and observed them until we were fairly certain of the approximate location of each nest burrow. If multiple pairs of owls were nesting within the colony, we assigned a number to each pair and used a random number generator to determine which nest would be used for data collection.

We identified a nest burrow by the presence of at least two of the following signs: owl at burrow entrance, entrance lined with shredded manure of cattle or other grazing mammals, owl droppings, and regurgitated pellets or other prey remains (Thompson 1984, Griebel and Savidge 2007, Lantz et al. 2007). Burrowing Owls often line the nest burrow entrance with shredded manure (Butts and Lewis 1982, Levey et al. 2004, Smith and Conway 2007), and we used the presence of shredded manure as the deciding factor for identifying the nest burrow if several burrows in a small area contained signs of owls.

If the prairie dog colony did not contain any Burrowing Owls, we chose a random burrow within the visible colony boundaries. We used a method described by Restani et al. (2001) where we broke the colony down into progressively smaller quadrants selected at random. We continued to select quadrants until a single suitable burrow remained. Only burrows ≥5 cm in diameter (Lantz et al. 2007) and unobstructed for ≥0.5 m were selected. Virtually all prairie dog burrows in our study area exceeded the minimum diameter criterion, but some randomly selected burrows were rejected because they had collapsed.

To evaluate the vegetative composition around the burrow, we placed pin flags at 2 m and 4 m from the burrow in each cardinal direction. We centered a 1-m^2 Daubenmire frame (Daubenmire 1959) over each flag and recorded the cover class for bare ground (i.e., exposed soil), grass, forb, and tree/shrub. Cover classes were defined as Class 1, 0–5%; Class 2, 5–25%; Class 3, 25–50%; Class 4, 50–75%; Class 5, 75–95%; and Class 6, 95–100%. Total coverage for all cover types could sum to >100%, because vegetation frequently grows in overlapping layers. We calculated the mean value for percent cover of each cover type near a selected burrow using the midpoint for each recorded cover class (Daubenmire 1959).

We obtained a visual obstruction reading using a modified Robel pole (Robel et al. 1970) marked in increments of 0.5 dm. The pole was placed 5 m north of the burrow and viewed from a height of 1 m at a distance of 4 m in each cardinal direction. The lowest mark on the pole that was not completely obstructed by vegetation was recorded. This process was repeated with the pole placed 5 m east, south, and west of the burrow. We

calculated the mean value of the 16 visual obstruction readings taken around each burrow.

We measured the distance to the nearest active burrow, or burrow currently being used by prairie dogs, and the nearest inactive burrow. An active burrow was identified by the presence of fresh scat, fresh digging, clipped vegetation, or a prairie dog at the burrow entrance; an inactive burrow had unclipped vegetation in or near the burrow entrance, had spider webs growing across the burrow entrance, and/or lacked fresh scat (Desmond et al. 1995, Desmond and Savidge 1996, Lantz et al. 2007). We also counted the total number of active and inactive burrows within 10 m of the selected burrow.

We measured the distance to the nearest vegetational edge. The edge was defined as the zone where prairie dogs were no longer modifying the vegetation by grazing or clipping it. The nearest edge was often the outer perimeter of the colony, but occasionally prominent vegetational edges were found within the boundaries of the colony, often because saturated soil excluded prairie dogs and caused a different plant community to develop.

Distance to the nearest perch was measured. We considered a perch to be any object ≥0.5 m tall that could support a Burrowing Owl (Lantz et al. 2007). We did not consider prairie dog mounds to be perch sites since they were abundant at almost all sites and burrow density and distance to burrows were already measured.

Colony- and Landscape-Level Data Collection.—We quantified colony- and landscape-level metrics using a geographic information system (GIS; ArcMAP version 9.3, Esri, Redlands, California, USA). We used 2010 National Agriculture Imagery Program (NAIP) aerial photographs and ground truthing to digitize the boundaries of the prairie dog colonies. The GIS calculated the area of each colony.

The GIS was used to measure the distance to the nearest road. Roads varied from minimum-maintenance trails to paved highways, but we only considered roads with bare surfaces (i.e., we did not include infrequently used pasture access trails with vegetated wheel tracks). If the nearest road was ≥600 m away, we recorded the distance as 600 m. This maximum distance approximated the home range size of Burrowing Owls calculated by previous studies (Green and Anthony 1989, Haug and Oliphant 1990, Sissons et al. 2001, Gervais et al. 2003).

Buffers with radii of 400 m and 800 m were created around each selected burrow. These buffer sizes were based on home ranges of Burrowing Owls and typical scales of land management (e.g., crop field sizes). Within each buffer, we digitized trees, grassland, cropland (i.e., row crops and small grains), and hayland using NAIP photographs and ground truthing. We used GIS to calculate percent cover of trees, grassland, cropland, and hayland within each buffer. Only colonies with non-overlapping buffers were used in analyses.

Statistical Analyses.—We used logistic regression and the information-theoretic approach to evaluate the influence of local, colony, and landscape variables (Appendix 1) on nest site selection by Burrowing Owls. We developed *a priori* models in three single-scale subsets—local, colony, and landscape—using combinations of variables based on existing literature and prior observations of nest sites in western South Dakota (Appendix 2). We did not include two variables in the same model if they had a Spearman rank correlation ≥0.5. For models in the landscape subset, we followed the approach of Cunningham and Johnson (2006) and created separate models at both buffer sizes for the same variable (e.g., if a model contained percent tree cover within 400 m of the burrow, we also included another version of the same model but substituted percent tree cover within 800 m of the burrow). The response variable for binary logistic regression was nest presence/absence.

We used the program SYSTAT (2007) for all modeling and statistical analyses. Akaike's Information Criterion, corrected for small sample sizes (AIC_c; Burnham and Anderson 2002), was used to rank the models in each subset according to the level of support. We calculated the AIC_c difference (ΔAIC_c) between the model with the lowest AIC_c value in each subset and all other models in the subset. According to Burnham and Anderson (2002), models with $\Delta AIC_c < 2$ have 'substantial' support for being the best model in a set. Models with $\Delta AIC_c < 2$ were retained from each subset and combined in four multiscale model subsets—local + colony, local + landscape, colony + landscape, and local + colony + landscape. We ranked the retained single-scale models and the multiscale models by ΔAIC_c and considered any model with $\Delta AIC_c < 2$ to be competitive as the best model in the entire set unless it differed from the top model only by the

TABLE 1. Competitive nest site selection models ($\Delta AIC_c < 2$) for Burrowing Owls, the lowest ΔAIC_c model from each model subset, and the null model (intercept only). Data were collected during the summer of 2011 at Burrowing Owls' nest burrows and random non-nest burrows in prairie dog colonies ($n = 107$) located throughout western South Dakota. ROC is the area under the receiver operating characteristic curve, and ρ^2 is the McFadden's rho-squared value. Variable descriptions are found in Appendix 1.

Model	Model subset	ΔAIC_c	ρ^2	ROC
FORB + BARE + ROBEL + TREE_800	Local + Landscape	0	0.297	0.822
FORB + ROBEL + TREE_800	Local + Landscape	1.137	0.269	0.812
FORB + ROBEL + COL_AREA + TREE_800	Local + Colony + Landscape	2.874	0.273	0.816
ROAD + TREE_800	Landscape	12.781	0.155	0.721
COL_AREA + ROAD + TREE_800	Colony + Landscape	13.557	0.166	0.731
FORB + BARE + ROBEL	Local	14.701	0.157	0.738
FORB + BARE + ROBEL + COL_AREA	Local + Colony	15.961	0.165	0.750
COL AREA	Colony	26.470	0.024	0.638
Null	–	27.307	–	–

presence of an additional variable (Burnham and Anderson 2002, Arnold 2010). We calculated Akaike model weights to evaluate the relative support for each model (Burnham and Anderson 2002).

AIC values only indicate the relative strength of models in a set (Burnham and Anderson 2002, Cunningham and Johnson 2006), so we also considered McFadden's ρ^2 and area under receiver operating characteristic (ROC) curve as metrics of model fit and performance when evaluating competitive models. McFadden's ρ^2 is a metric of model fit; values from 0.2–0.4 are considered highly satisfactory (Tabachnick and Fidell 2007). We used ROC curves to evaluate the ability of each model to discriminate between nest burrows and non-nest burrows. Hosmer and Lemeshow (2000) considered models with area under ROC curve values between 0.7–0.8 to have 'acceptable discrimination' and those with values between 0.8–0.9 to have 'excellent discrimination.'

We also evaluated the effects of variables within competitive models. We calculated a relative importance value for each variable that appeared in one or more competitive models by summing the Akaike weights of models that contained the variable (Burnham and Anderson 2002). Because models containing landscape variables were duplicated at different scales, importance values for landscape variables are not directly comparable to those for local and colony variables. We calculated 85% confidence intervals for the coefficient of each variable in competitive models (Arnold 2010). If the confidence interval overlapped zero, the variable had no significant effect.

RESULTS

Within our sample of 107 prairie dog colonies, 80 were occupied by Burrowing Owls and 27 were unoccupied. Fifty-three occupied colonies contained two or more nests.

Two *a priori* models, both from the local + landscape subset, were considered competitive by having $\Delta AIC_c < 2$ (Table 1). The competitive models had highly satisfactory fit and excellent discrimination (Table 1), but model weights were relatively low (0.209 and 0.119). All variables in competitive models had significant effects.

Probability of a site being chosen for nesting dropped from >80% with 0% tree cover within 800 m to below 50% with an increase to 3.5% tree cover (Fig. 2). Both competitive models contained percent tree cover within 800 m of the burrow (TREE_800). Models at the 400 m scale were not competitive. The importance value for TREE_800 was 0.906.

Burrowing Owls were most likely to nest where visual obstruction was low and percent cover of forbs and bare ground was relatively high (Fig. 2). Average visual obstruction reading (ROBEL) occurred in both competitive models. ROBEL had an importance value of 0.998. Average forb cover (FORB) appeared in both competitive models and average bare ground cover (BARE) appeared in the top model, but both FORB and BARE were considerably less important (importance values of 0.574 and 0.373, respectively) than TREE_800 and ROBEL, and they had relatively weak effects (Fig. 2).

DISCUSSION

Our results indicate that Burrowing Owls' nest site selection in prairie dog colonies is related to

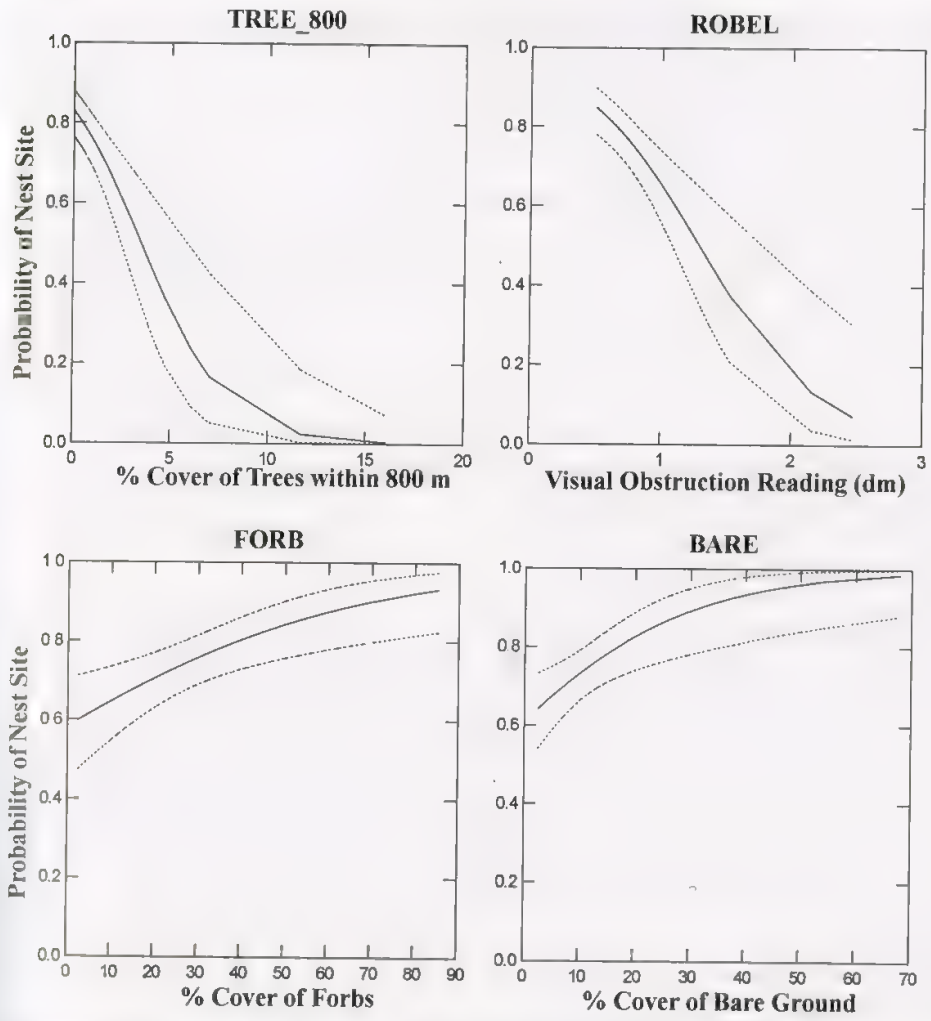

FIG. 2. Effects of variables included in the top model for nest site selection by Burrowing Owls in western South Dakota. Dotted lines represent 85% confidence intervals. Data were collected during the summer of 2011 at Burrowing Owls' nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota.

both local and landscape habitat characteristics. Single-scale models were not competitive with multiscale models, suggesting that Burrowing Owls may seek out prairie dog colonies in suitable landscapes before searching for specific local vegetative characteristics around potential nest burrows.

Burrowing Owls in western South Dakota avoid trees when selecting prairie dog colonies to nest within. Prairie dogs typically establish colonies in upland areas that are relatively free of trees (Hygnstrom and Virchow 1994), so tree cover is generally absent within and near colonies. However, Burrowing Owls in our study avoided selecting colonies for nest sites where trees were more abundant outside of the colony. Although Burrowing Owls frequently hunt within their selected prairie dog colonies, their home ranges often extend beyond the boundaries of prairie dog colonies, where other prey are available (Butts 1973; Orth and Kennedy 2001; JPT, pers. obs.). The better performance of models at the 800 m scale over models at the 400 m scale indicates that Burrowing Owls select against trees within their home ranges and perhaps beyond.

Our results indicate that even small increases in tree cover can have disproportionately negative effects on Burrowing Owl nest site selection. A variety of grassland birds respond negatively to the presence of trees (Bakker 2003), but our study

is the first to demonstrate a negative relationship between trees and Burrowing Owls. Stevens et al. (2011) also looked at the effects of tree cover but did not find it to be an important predictor of Burrowing Owls' home ranges in southeastern Alberta and southern Saskatchewan; however, tree cover was much lower in their study area (mean of 0.3% within 1,200 m) than in our study area (mean of 1.0% within 800 m). Burrowing Owls may avoid trees in the landscape because trees provide perch sites and nest sites for larger species of raptors. We did not witness any predation events, but we did find remains of Burrowing Owls that had been killed by avian predators. The most abundant large raptors observed near prairie dog colonies in our study area were Red-tailed Hawks (*Buteo jamaicensis*), Swainson's Hawks (*B. swainsonii*), Ferruginous Hawks (*B. regalis*), and Great Horned Owls (*Bubo virginianus*). Habitat for these raptors includes wooded draws or other patches of trees surrounded by upland prairie (Faanes 1983; Johnsgard 1990, 2002), and all of these species are known or suspected predators of Burrowing Owls (Konrad and Gilmer 1984, Clayton and Schmutz 1999, Leupin and Low 2001, Todd 2001, Davies and Restani 2006, Poulin et al. 2011). Birds should be expected to select breeding sites that minimize predation risk for themselves and their offspring (Lima 2009), and trees increase the risk to Burrowing Owls.

The amount of grassland in the surrounding landscape had no influence on nest site selection by Burrowing Owls in our study, suggesting that, at current levels, the conversion of grassland to cropland or hayland is not limiting Burrowing Owls' nest site selection. The landscape in western South Dakota still consists of predominantly intact grasslands, especially in areas where prairie dog colonies remain. The local vegetation variables included in competitive models suggest that Burrowing Owls may nest in areas of high prairie dog activity within colonies. The digging, scratching, grazing, and clipping behaviors of prairie dogs reduce visual obstruction by favoring short, grazing-tolerant grasses, create more patches of bare ground, and promote annual forbs (Agnew et al. 1986, Archer et al. 1987, Whicker and Detling 1988, Winter et al. 2002). Selection of nest sites with short, sparse vegetation is consistent with results of previous studies that have recorded visual obstruction measurements (Green and Anthony 1989, Clayton and Schmutz 1999). Several factors may explain why Burrowing Owls tend to nest in areas with low visual obstruction. Unlike more nocturnal owl species that rely heavily on their sense of hearing to locate prey, Burrowing Owls are primarily visual hunters (Johnsgard 2002). Burrowing Owls use a variety of hunting methods, including running after prey on the ground, flying from a perch, and hovering (Butts 1973, Clayton and Schmutz 1999, Johnsgard 2002, Poulin et al. 2011). These hunting methods are more likely to be successful when vegetation is short and relatively sparse. Burrowing Owls may have difficulty locating prey at ground level if visual obstruction is high, which could have particularly strong implications for juvenile owls, since they often hunt for insects from the ground (JPT, pers. obs.). Low visual obstruction near the nest burrow may also be important for predator detection (Green and Anthony 1989).

We suspect that the strong influence of visual obstruction on nest site selection may have been, at least in part, a result of above-average precipitation in western South Dakota during our study. Precipitation may influence the heterogeneity of vegetation within prairie dog colonies. Vegetation will grow faster and taller in wet years, causing more dramatic differences between clipped and unclipped vegetation (Plumpton and Lutz 1993, Lomolino and Smith 2003, Tipton et al. 2008). The presence of prairie dogs may be especially important for Burrowing Owls seeking nest sites in wet years, when unclipped vegetation would exclude Burrowing Owls from otherwise suitable burrows.

Nest sites of Burrowing Owls in western South Dakota are associated with a relatively high abundance of forbs and bare ground. Despite the comparatively weak effects of these variables, their presence in competitive models may indicate biological significance. Thompson (1984) and MacCracken et al. (1985) found that forb cover was greater around nest burrows than around random burrows in central Wyoming and southwestern South Dakota, respectively, but bare ground cover did not differ between nest burrows and random burrows in either study area. In contrast, Plumpton and Lutz (1993) found no differences in forb cover around nest burrows and random burrows in north-central Colorado, but nest burrows were surrounded by more bare ground than random burrows.

Our findings improve the understanding of how landscape scale habitat features influence nest site

selection by Burrowing Owls. Conservation of the Burrowing Owl in western South Dakota, and elsewhere in the Great Plains, may depend on preserving open landscapes with few trees in order to provide suitable habitat. Even low levels of tree cover in the landscape can make a prairie dog colony unsuitable for nesting by Burrowing Owls, regardless of local vegetation characteristics. Land managers should avoid planting trees in or near areas occupied by Burrowing Owls or by areas with high potential as habitat for Burrowing Owls. Managers should also prevent the colonization of upland habitats by trees such as eastern red cedar. Promoting the persistence of active prairie dog colonies, which provide the vegetative characteristics selected by Burrowing Owls, is critical to maintaining the Burrowing Owl as a relatively common component of the Great Plains' avifauna.

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APPENDIX 1. Habitat variables collected in 2011 at Burrowing Owls' nest burrows and random non-nest burrows in prairie dog colonies in western South Dakota for use in nest site selection models. Variables with the same superscripts were correlated (Spearman rank correlation ≥0.5) and were not used together in the same model. Variables marked with an asterisk (*) were not used in any *a priori* models because of correlations with other variables predicted to be more important based on the available literature.

Variable	Description	Mean	SE	Range
ACTIVE[a,b]	Number of active prairie dog burrows within 10 m	2.551	0.215	0–9
INACTIVE[c,d]*	Number of inactive prairie dog burrows within 10 m	2.963	0.267	0–13
TOTAL_BURROWS[a,c,e]	Total number of prairie dog burrows within 10 m	5.514	0.342	0–19
NEAR_ACTIVE[b]	Distance in m to the nearest active prairie dog burrow	11.093	1.650	1.2–100
NEAR_INACTIVE[d,e]*	Distance in m to the nearest inactive prairie dog burrow	6.897	0.431	1.2–30.1
GRASS[f]*	Estimated % cover for grass	59.229	1.812	8.75–91.25
FORB[f]	Estimated % cover for forbs	31.352	2.194	2.50–85.31
BARE	Estimated % cover for bare ground	13.817	1.300	2.50–67.81
ROBEL	Average visual obstruction reading in dm	0.756	0.037	0.50–2.47
EDGE	Distance in m to the nearest vegetational edge	33.223	3.195	0–181.4
PERCH	Distance in m to the nearest potential elevated perch site	125.779	11.325	0–600
COL_AREA	Area of the prairie dog colony in ha	37.154	6.284	0.48–426.69
ROAD	Distance in m to the nearest road	301.636	18.014	2–600
GRASS_400[g,h]	% cover of grassland within 400 m	89.002	1.316	44.22–100.04
GRASS_800[g,i,j]	% cover of grassland within 800 m	81.172	1.803	30.75–99.85
CROP_400[h,i,k]	% cover of cropland within 400 m	4.578	1.049	0–48.30
CROP_800[i,k]	% cover of cropland within 800 m	8.133	1.433	0–55.12
HAY_400[j]	% cover of hayland within 400 m	0.947	0.476	0–40.73
HAY_800[j]	% cover of hayland within 800 m	2.504	0.678	0–53.34
TREE_400[m]	% cover of trees within 400 m	0.619	0.173	0–10.75
TREE_800[m]	% cover of trees within 800 m	1.000	0.230	0–16.06

APPENDIX 2. Single-scale *a priori* nest site selection models for Burrowing Owls in western South Dakota, 2011. Models are in three subsets representing different spatial scales—local, colony, and landscape. Models in bold typeface had $\Delta AIC_C < 2$ within the subset and were retained in multiscale models. Variable descriptions are found in Appendix 1.

Local subset	Colony subset	Landscape subset
FORB	**COL_AREA**	ROAD
BARE		GRASS_400
ROBEL		GRASS_800
ACTIVE + ROBEL		**TREE_400**
TOTAL_BURROWS + ROBEL		**TREE_800**
TOTAL_BURROWS + EDGE		ROAD + CROP_400
FORB + ROBEL		ROAD + CROP_400
BARE + ROBEL		ROAD + HAY_400
ROBEL + PERCH		ROAD + HAY_800
ACTIVE + FORB + ROBEL		**ROAD + TREE_400**
TOTAL_BURROWS + ROBEL + PERCH		**ROAD + TREE_800**
TOTAL_BURROWS + EDGE + PERCH		GRASS_400 + TREE_400
NEAR_ACTIVE + FORB + EDGE		GRASS_800 + TREE_800
NEAR_ACTIVE + BARE + EDGE		CROP_400 + TREE_400
FORB + BARE + ROBEL		CROP_800 + TREE_800
		HAY_400 + TREE_400
		HAY_800 + TREE_800
		CROP_400 + HAY_400 + TREE_400
		CROP_800 + HAY_800 + TREE_800

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DIET OF MEXICAN SPOTTED OWLS IN UTAH AND ARIZONA

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ABSTRACT.—Mexican Spotted Owls (*Strix occidentalis lucida*) occupy forest-dominated environments but also inhabit rocky canyonlands. I studied the owls' diet in canyon habitats in southern Utah and northern Arizona (1991–2007), and in mixed-conifer forest in the Rincon Mountains of southeast Arizona (1996–1997). I identified 3,315 prey items in regurgitated pellets from 38 pairs of owls in canyon habitat, and 383 prey items from 5 pairs in the Rincon Mountains. In canyons and forests, vertebrates dominated owl diets (97–99% of total prey biomass) with mammals accounting for 91–92% of prey biomass. In canyons, mammalian prey was primarily woodrats (*Neotoma* spp., 79% biomass), followed by white-footed mice (*Peromyscus* spp., 11%), and cottontail rabbits (*Sylvilagus* spp., 5%). In forest habitat, woodrats comprised 54% of biomass, followed by Botta's pocket gophers (*Thomomys bottae*, 13%), and cottontail rabbits (11%). For nine owl territories in three canyon regions in Utah, diets varied among the owl pairs with contribution to total prey biomass by woodrats ranging from 65–91%, typically followed by white-footed mice ranging from 13–19%. In both canyon and forest study areas, a variety of prey were consumed in addition to murids, including rabbits, pocket gophers, sciurids (*Tamias* spp.), heteromyids (e.g., *Perognathus* spp.), various bats (Vespertilionidae), shrews (*Sorex* spp.), small passerine birds, and numerous arthropods. *Received 6 February 2013. Accepted 7 April 2013.*

Key words: Arizona, canyons, diet, habitat, Mexican Spotted Owl, *Strix occidentalis lucida*, Utah.

While the Mexican Spotted Owl (*Strix occidentalis lucida*) is typically associated with forest environments in the southwestern United States (Ganey and Balda 1989, May et al. 2004), it is also found in rocky canyons of the Colorado Plateau (Kertell 1977, Rinkevich 1991, Willey 1998). The Mexican Spotted Owl was listed as threatened by the US Fish and Wildlife Service in 1993 (Cully and Austin 1993, USDI 1995). Most field studies have focused on forest environments, with less attention to rocky canyon habitats (Mullet and Ward 2010, USDI 2012). Previous studies in canyonlands have addressed distribution (Willey 1998), juvenile dispersal (Willey and van Riper 2000), home range characteristics (Willey and van Riper 2007, Bowden 2008), and territorial occupancy (Hockenbary 2011). However, diet studies have occurred primarily in forest-dominated habitats, where woodrats (*Neotoma* spp.) or mice (*Peromyscus* spp.) typically comprised the greatest percentage of prey (Ganey 1992, Ward and Block 1995, Young et al. 1997, Block et al. 2005). Few studies investigated diet composition in rocky canyonlands (Wagner et al. 1982, Rinkevich 1991, Ganey 1992), thus less is known about food habits of Mexican Spotted Owls outside forest environments.

Mexican Spotted Owls are sit-and-wait ambush predators that primarily consume small mammals, and occasionally birds, reptiles, and various arthropods (USDI 2012). My goal was to describe Mexican Spotted Owl diets among the primary subpopulations representing rocky canyon habitat in southern Utah and northern Arizona. For comparison, I also included diet information from a forest location in southeast Arizona. My specific objectives were: 1) describe general characteristics of the Mexican Spotted Owl's diet in canyon habitat, 2) estimate the relative frequency and biomass of prey in taxonomic categories, and 3) compare the diets of canyon and forest study areas.

METHODS

Study Area.—Regurgitated pellets were collected at canyon roost sites located in the principal Mexican Spotted Owl subpopulations of southern Utah (Willey 1998) and northern Arizona (Bowden 2008). Pellets were also collected at a forested study area in southeast Arizona, the Rincon Mountains. The canyon study areas in Utah included: Zion National Park (Zion) located 35 km west of Kanab; Paria River (Paria) located 45 km east of Kanab; Capitol Reef National Park (Reef) located 25 km northeast of Torrey; Canyonlands National Park (Canyon) located 60 km southwest of Moab; and the Manti La Sal (Manti) study area was 35 km west of Blanding. In northern Arizona, the Grand Canyon National Park study area (Grand) was located 124 km northwest of Flagstaff, in northern Arizona. All of the canyon study areas represented similar topography, with maze-like canyons eroded into

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cliff-forming sedimentary formations (Thornbury 1965). Elevations ranged from 1,345–2,445 m, and vegetation depended strongly on topography and surface geology (Brown 1982, Huisinga et al. 2006). Canyon floors with intermittent surface water contained patches of riparian vegetation, including willow species (*Salix* spp.), boxelder (*Acer negundo*), bigtooth maple (*A. grandidentatum*), and Fremont cottonwood (*Populus fremontii*). In relatively cool microsites were small patches of mixed-conifer forest including Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and Ponderosa pine (*Pinus ponderosa*). Along xeric canyon bottoms, desert scrub or two needle pinyon (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) were common, and desert scrub often included blackbrush (*Coleogyne ramosissima*), various cacti (*Opuntia* spp.), and scattered bunch grasses, e.g., indian ricegrass (*Stipa hymenoides*). All canyon study areas are part of the high plateaus subsection of the Colorado Plateau physiographic province (Thornbury 1965), where total annual precipitation averaged 17 cm during the study, and temperature ranged from −1.4 to 44 °C (National Weather Service archives, Salt Lake City, Utah, USA).

The study area of the Rincon Mountains (Rincons) was located 12 km east of Tucson, Arizona in Saguaro National Park, and encompassed 25,000 ha of roadless areas that formed a montane island surrounded by desert. The Rincons range in elevation from 1,988–2,599 m, and average annual precipitation was 760 mm at the summit of Mica Mountain. Precipitation occurred in two seasons, with thunderstorms during July and August providing ~60% of annual rainfall, and the remainder as snow during December to March (Saguaro National Park, unpubl. climate records). In the Rincons, Mexican Spotted Owls occurred at the highest elevations dominated by Petran Montane Conifer Forest (Brown 1982), with Douglas fir, white fir, Ponderosa pine, southwestern white pine (*P. strobiformis*), and several oaks (mostly *Quercus gambelii, Q. hypoleucoides*, and *Q. arizonica*). Mixed grasses, herbaceous species, and bracken fern (*Pteridium aquilinum*) were present as understory.

Locating Owl Roosts and Pellets.—Surveys for Mexican Spotted Owls were conducted using a standard protocol (Forsman 1983) during March to July in the canyon study areas (1991–2007) and in the Rincons (1996–1997). After owls were audibly detected, diurnal visits were conducted to search for roost sites, and pellets were collected opportunistically during March to September. Pellets were collected at roost areas for five owl pairs in the Rincons during 1996–1997. In the canyons, pellets were collected during 1991–1995 for seven pairs at Zion, ten pairs at Reef, five pairs at Manti, and four pairs at Canyon. In addition, pellets were collected for four pairs at Paria during 2001–2007, and eight pairs in Grand Canyon during 2004–2006. All pellets collected during a visit to a roost area were treated as a single sample because remains of prey may appear in more than one pellet scattered among nearby roosts (Ganey 1992). Roost areas of adjacent owl pairs were ≥2 km apart, thus single samples did not include pellets from multiple pairs. Vertebrate prey remains were identified by comparison with reference specimens (Montana State University, Natural History Collection) and a taxonomic key of prey remains. The minimum number of individuals of each taxa were determined for each sample by counting identifiable remains (Marti 1988, Ganey 1992).

Diet was expressed as relative frequency and relative biomass converted to percent of total for each index, with all roost sites combined for each study area in the overall analysis, or for each owl pair in the territory analysis. Average body mass estimates were obtained from the literature (Forsman et al. 1984, Block et al. 2005), field specimens (Willey and Willey 2010), and reference specimens (Montana State University). Given the similarity of rodent fauna among the canyon study areas (Rosenstock 1996, Willey and Willey 2010), I assumed mass measurements taken in the field (Willey and Willey 2010) were representative of the region (Appendix 1).

Roost sites were visited opportunistically, resulting in differing sample frequencies among years and study areas, and likely caused unknown biases. Because relatively large prey collections are necessary for statistical analyses among "treatments" (Marti 1988), I elected not to conduct statistical contrasts of diet among habitats, years, or territories, and did not formulate *a priori* hypotheses concerning diet differences among study areas (Cherry 1998). Rather, my objective was to describe general aspects of diet among study areas and a select group of canyon territories with relatively high samples collected during sequential years (Ganey 1992).

TABLE 1. Relative % contribution of prey to diet of Mexican Spotted Owls in canyon and forest study sites, from Utah and Arizona, 1991–2007.

Prey[a] (No. prey items)	Forest site	Canyon sites						
	Rincons (383)	Manti (645)	Zion (370)	Grand (101)	Paria (667)	Reef (984)	Canyon (548)	Overall (3,315)
woodrats	13.6	23.9	34.6	58.4	48.7	29.4	37.6	35.0
white-footed mice	15.4	25.8	27.8	24.7	22.6	38.8	35.4	30.8
Botta's pocket gophers	4.2	0.2	0.8	0.0	0.3	0.1	0.0	0.2
bats	3.4	1.2	2.7	3.0	3.1	3.0	8.2	3.5
rabbits	1.0	0.0	1.1	1.0	1.5	0.1	0.7	0.9
other mammals	1.3	5.8	3.0	0.0	2.6	4.8	1.5	3.7
birds	6.8	1.9	3.0	4.0	1.3	1.5	1.8	1.7
reptiles	0.5	0.0	0.0	0.0	0.3	0.6	1.5	0.5
arthropods	53.8	41.2	27.0	8.9	19.6	21.7	13.3	23.7

[a] See appendix 1 for complete list of common and scientific names of prey.

RESULTS

I identified 3,315 prey items from pellets of 38 pairs of Mexican Spotted Owls in canyon areas and 383 prey items from pellets of five pairs of owls in the forested Rincons (Table 1). For canyons, owls consumed at least 21 species of mammals, four species of birds, one species of reptile, and several arthropods (Appendix 1). In the Rincons, the diet included at least 10 species of mammals, three species of birds, one reptile, and various arthropods (Table 1).

Vertebrates dominated the diet in canyons, comprising 59–91% of total prey. For the mammalian prey consumed in canyons, the desert woodrat (*N. lepida*) was most frequent, followed by the brush mouse (*P. boylii*). The owls occasionally took voles (*Microtus* spp.), chipmunks (*Tamias* spp.), shrews (*Sorex* spp.), desert cottontails (*Sylvilagus audubonii*), various bats (Vespertilionidae), and Botta's pocket gophers (*Thomomys bottae*) (Table 1). In the Rincons, the pinyon mouse (*P. truei*) was taken most frequently, followed by the Mexican woodrat (*N. mexicana*), and pocket gopher. In addition to vertebrate prey, invertebrates were consumed in high numbers in the Rincons (54% of total prey) (Table 1), including Coleoptera, Cicadoidea, Araneae, Scorpiones, Stenopelmatidae, and Gryllidae. In the canyons, owls also consumed relatively large numbers of arthropods (24% of total prey), including Coleoptera, Araneae, Scorpiones, and Stenopelmatidae.

Across all study areas, vertebrates dominated the diet in terms of biomass, comprising 97–99% of total prey biomass (Table 2), and mammals accounted for 91–92% of prey biomass. Although

TABLE 2. Relative % biomass composition of prey for Mexican Spotted Owl diets in canyon and forest study sites, Utah and Arizona, 1991–2007.

Prey[a] (total g)	Forest site	Canyon sites						
	Rincons (13,481)	Manti (27,423)	Zion (23,115)	Grand (9,442)	Paria (54,457)	Reef (56,271)	Canyon (36,319)	Overall (207,027)
woodrats	54.3	79.2	78.4	88.1	83.0	72.4	80.0	78.9
white-footed mice	9.6	13.4	9.8	5.8	6.1	13.5	11.3	10.9
Botta's pocket gophers	13.4	0.4	1.5	0.0	0.4	0.2	0.0	0.4
bats	1.5	0.4	0.7	0.5	0.5	0.8	1.4	0.9
rabbits	11.6	0.0	6.8	4.1	6.1	6.9	4.3	5.5
other mammals	0.6	3.4	0.5	0.0	3.1	4.8	0.8	1.7
birds	5.8	1.3	1.4	1.3	0.5	0.6	1.4	0.8
reptiles	0.2	0.0	0.0	0.0	0.0	0.1	0.4	0.1
arthropods	3.0	1.9	0.9	0.2	0.4	0.7	0.4	0.8

[a] See appendix 1 for list of common and scientific names, and prey biomass sources.

TABLE 3. Territorial variation in the diet of Spotted Owls in three canyon study areas in Utah, including Capitol Reef and the Manti La Sal (1994–1995); and the Paria River (2005–2006). Values are % of total prey biomass (g) consumed 1 March to 31 August (n = total prey items, Mass = total biomass).

			Prey type[a]					
Study area	Site	*n*	*Neotoma*	*Peromyscus*	*Sylvilagus*	Other mammals	Other	Mass
Capitol Reef	Mile	138	74.2	13.6	5.1	5.7	1.4	7,606 g
	Burr	158	64.9	16.5	9.0	7.7	2.0	8,693 g
	Firs	260	71.5	17.3	7.2	2.8	1.1	16,174 g
	Uspr	191	70.7	19.2	4.2	7.8	1.1	9,380 g
Manti La Sal	Dark	256	68.0	11.4	13.9	4.0	2.7	11,198 g
	Peav	217	80.3	14.4	0.0	4.1	1.2	11,595 g
Paria River	Hogi	164	91.4	3.7	2.6	1.5	0.9	14,968 g
	Snak	212	87.3	3.5	7.3	1.1	0.4	21,308 g
	Star	243	76.6	8.9	9.7	3.4	1.3	16,017 g

[a] Prey types: "Other mammals" included various rodents (voles, pocket mice, kangaroo rats, chipmunks), bats, and pocket gophers; "Other" included birds and arthropods. See appendix 1 for common and scientific names, and mass estimates.

birds, reptiles, and arthropods were taken, they contributed little (<2%) in terms of prey biomass in the canyons; however, birds comprised 6%, and arthropods 3% of biomass in the Rincons, respectively (Table 2). In all canyon study areas combined, woodrats contributed 79% of total biomass, followed by white-footed mice, and cottontail rabbits. However, in the Rincons, woodrats comprised 54% of biomass, followed by pocket gophers, and rabbits (Table 2). Unlike the canyon areas, white-footed mice contributed relatively lower biomass (<10%) in the Rincon Mountains. Across all study areas, I observed that the owls consumed diverse prey, including small Jerusalem crickets (Stenopelmatidae; ca. 1 g) up to adult Desert cottontail rabbits (ca. 390 g). Mean prey mass for all prey items in the Rincons was 35 g (SE = 6.1), and ranged from 43–94 g (overall mean = 63 g, SE = 1.8) in canyon habitats.

I described the diet for nine owl territories with the largest samples in consecutive years for canyon habitats, including Reef and the Manti during 1994–1995, and the Paria during 2005–2006 (Table 3). Woodrats provided the main contribution to biomass consumed by owls in all territories, ranging from 65–91% total biomass (Table 3). During 1994–1995, white-footed mice were the second highest contributor to biomass at five territories; however, rabbit biomass exceeded mice at one site, where they contributed 14% of total biomass at Manti (Table 3). In the Paria, rabbits were the second highest contributor to biomass at two territories, and overall, white-footed mice contributed relatively less to owl diets than observed in the Reef or Manti. The contribution to biomass by other mammal species (e.g., gophers, chipmunks, and bats) was typically <4%, and birds and arthropods combined comprised <3% of biomass (Table 3). However, at Reef, chipmunks comprised up to 7% of biomass, showing a relatively high contribution for those years sampled.

DISCUSSION

Spotted Owls consumed a variety of prey in canyon and forest habitats, but nocturnal small mammals dominated the diet in the canyons, and in the forested Rincons (Table 2). Owls inhabiting rocky canyons primarily consumed woodrats, whereas owls in the Rincons preyed heavily on white-footed mice, but also consumed substantial numbers of arthropods, nearly twice the frequency observed in canyons (Table 1). The average prey mass (63 g) for canyons in my study was smaller than average masses reported for two similar canyon habitats in northern Arizona (111 g and 118 g, for Walnut Canyon and Black Mesa, respectively) reported by Ganey (1992). When I generated estimates with only vertebrate prey, eliminating the influence of arthropods (Block et al. 2005), the average prey mass for canyons in Utah was 91 g. My estimate of mean mass based on only vertebrate prey was greater than values reported for forested environments in Arizona by Ganey (1992), and Block et al. (2005), 70 g, and 40 g, respectively. Mean prey mass in the Rincons, with relatively high frequency of arthropods (54% of total prey) was 35 g, but increased to 74 g for only vertebrate prey. For

California Spotted Owls (*S. o. occidentalis*) in forest environments, Barrows (1980) reported an average prey mass >100 g. Forsman et al. (1984), working on Northern Spotted Owls (*S. o. caurina*) in Oregon, reported a range of 54–150 g, and Forsman et al. (2004), also working in Oregon, found average prey size was 117 g (SE = 6.5).

The high frequency of woodrats that I observed in the diet of Spotted Owls in canyon study areas was consistent with other studies where food habits were surveyed in similar canyon environments (Wagner et al. 1982, Rinkevich 1991, Ganey 1992, Ward and Block 1995). However, in forest environments in Arizona, white-footed mice were the dominant prey species identified by previous studies (Ganey 1992, Block et al. 2005) and my sampling in the Rincon Mountains (Table 2). Working in forest environments in northern Mexico, Young et al. (1997) showed that various mice taxa were taken more frequently than woodrats by Spotted Owls.

I examined the diet among several owl territories located in canyon habitat in southern Utah, and observed the biomass of woodrats ranged from 65–91% among owl pairs (Table 3). Inter-territorial variation could represent local responses to prey availability, habitat differences, and demographic factors, all of which may interact with year and site-level covariates. Given the lack of samples (especially across years), and systematic sampling during my study, factors that contributed to the observed variation are unknown. I recommend that future studies of food habits in canyon environments utilize large systematic samples from focal pairs, with pellets collected across multiple years to explore sources of variation. Studies that concurrently investigate owl diet and prey ecology might be emphasized, because they would allow investigations of prey consumption versus availability (Block et al. 2005, USDI 2012). I recommend future studies focus on ecological processes that influence woodrats and white-footed mice because of their prominence in the diets of owls occupying canyon habitat. Furthermore, management activities that negatively influence these prey species should be identified and avoided. For example, Willey and Willey (2010) documented negative effects of livestock grazing on relative abundance of woodrats and white-footed mice in the Paria study area, and Rosenstock (1996) observed similar results in the Reef. Johnston and Anthony (2008), working in forest environments in Oregon, observed that small mammalian prey consumed by Northern Spotted Owls declined when cattle reduced vegetation cover, especially in riparian areas. Further investigations concerning habitat components that support woodrats in canyon habitats should be emphasized (Willey and Willey 2010, USDI 2012).

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APPENDIX 1. Common and taxonomic names of prey identified in regurgitated pellets collected under Mexican Spotted Owl roosts in Utah and Arizona, 1991–2007. Also shown are mass (g) estimates used in biomass calculations and sources for mass estimates. Standard deviation of mass (in parentheses) is shown for animals captured in our Paria study area (2001–2007).

Prey taxa [a]	Mass (g) estimate	Source[b]
Mammals		
Great Basin pocket mouse (*Perognathus parvus*)	17.3 (2.6)	1
Ord's kangaroo rat (*Dipodomys ordii*)	50.3 (5.3)	1
American deer mouse (*Peromyscus maniculatus*)	21.3 (5.5)	1
Canyon mouse (*P. crinatus*)	18.2 (1.6)	1
Brush mouse (*P. boylei*)	23.4 (4.6)	1
Pinyon mouse (*P. trueii*)	24.4 (14.1)	1
Western harvest mouse (*Rheithrodontomys megalotis*)	9.7	2
Western white-throated woodrat (*Neotoma albigula*)	133.5 (59.1)	1
Desert woodrat (*N. lepida*)	137.1 (25.2)	1
Mexican woodrat (*N. Mexicana*)	143.2	3
Bushy-tailed woodrat (*N. cinerea*)	153.4 (79.3)	1
Montane vole (*Microtus montanus*)	24.3 (2.3)	1
Cliff chipmunk (*Tamias doralis*)	54.0 (13.8)	1
Least chipmunk (*T. minimus*)	54.0	3
Botta's pocket gopher (*Thomomys bottae*)	113.0	2
Desert cottontail (*Sylvilagus audubonii*)	391.0	3
Merriam's shrew (*Sorex merriami*)	5.2	2
Little brown myotis (*Myotis lucifugus*)	7.0	2
Silver-haired bat (*Lasionycteris noctivagans*)	10.0	2
Big brown bat (*Eptesicus fuscus*)	15.0	2
Townsend's big-eared bat (*Plecotus townsendii*)	10.0	2
Pallid bat (*Antrozous pallidus*)	18.0	2
Birds		
small birds	30.0	4
medium birds	70.0	4
Reptiles		
Western fence lizard (*Sceloporus occidentalis*)	11.0 (1.60)	1
Arthropoda		
Arachnida: Araneae, Scorpiones	3.0	5
Coleoptera	1.0	5
Orthoptera: Stenopelmatidae, Gryllidae	1.0	5
Hemiptera: Cicadoidea	2.0	5

[a] Common and scientific names for mammals follow Feldhamer et al. (2003).

[b] Sources. (1) animals captured in the Paria study area, where >10 individuals per species were measured (Willey and Willey 2010); (2) specimens in the Montana State University, Department of Ecology Natural History Museum; (3) Block et al. (2005); (4) Forsman et al. (1984); and (5) M. A. Ivie, pers. com

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NESTING OF THE WHITE-THROATED WOODCREEPER *XIPHOCOLAPTES ALBICOLLIS*

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ABSTRACT.—We report on the breeding biology of the White-throated Woodcreeper (*Xiphocolaptes albicollis*), a species endemic to the Atlantic forest of South America, based on 16 nesting attempts in 11 cavities (9 natural tree cavities and 2 nest boxes) in Misiones, northeastern Argentina. Natural cavities were 3.3–8.3 cm in diameter and 46–103 cm in depth, and generated by decay processes (not woodpeckers) at heights of 3–17 m in live trees 29–106 cm in diameter at breast height. White-throated Woodcreepers laid 2–4 eggs on alternate days, on a bed comprised of bark flakes, leaf fragments and seed pods. Incubation bouts ($n = 3$) were more than 1 hr 40 mins. Incubation lasted 17 days and the nestling period 18–22 days, shorter than the congeneric Great Rufous Woodcreeper (*Xiphocolaptes major*). Both adults brought nest material, incubated the eggs, fed the nestlings, and removed fecal sacs; however, we suspect that the male contributed more to fecal sac removal. Both adults roosted in the cavity a few nights before eggs were laid, but only one adult did so during the incubation and nestling periods. Nestlings were fed arthropods and small vertebrates at an average rate of 3 visits/hr with no change in delivery rate over the nestling period. Adults defended their nests from four bird species but shared one cavity with a roosting female Helmeted Woodpecker (*Dryocopus galeatus*) throughout their incubation period. We confirm that the White-throated Woodcreeper exhibits biparental care like the Great Rufous Woodcreeper, the *Dendrocolaptes* and the *Lepidocolaptes*, but in contrast to *Sittasomus*, *Dendrocincla* and *Xiphorhynchus*. We recommend studies with banded individuals to determine the relative contribution of each parent. *Received 5 March 2013. Accepted 22 June 2013.*

Key words: Atlantic forest, cavity-nesting bird, incubation, nestling, parental care, White-throated Woodcreeper, *Xiphocolaptes albicollis*.

The woodcreepers (Furnariidae: Dendrocolaptinae) are a subfamily of Neotropical birds, all of which appear to nest in tree cavities (Marantz et al. 2003). Despite being widespread and often common inhabitants of South and Central American forests, little is known about the breeding biology of many of these birds (Narosky et al. 1983, Majewska and Oteyza 2013). The largest woodcreepers are in the genus *Xiphocolaptes*, which includes four allopatric species: Great Rufous Woodcreeper (*X. major*), Strong-billed Woodcreeper (*X. promeropirhynchus*), Moustached Woodcreeper (*X. falcirostris*), and White-throated Woodcreeper (*X. albicollis*; Ridgely and Tudor 2009, Derryberry et al. 2011). Among the *Xiphocolaptes*, natural nests have been described in detail only for the Great Rufous Woodcreeper, although three nests of the Strong-billed Woodcreeper were recently described from nest boxes (Marantz et al. 2003, Cockle et al. 2011b, Botero-Delgadillo and Olaciregui 2011).

White-throated Woodcreepers are endemic to the Atlantic forest of Brazil, Paraguay, and Argentina, and their breeding biology is poorly known. Adults with fully active gonads were collected in October in Brazil and November in Paraguay (Belton 1984, Madroño et al. 1997, M. Robbins in litt. 2013). Clutch has been reported as two white eggs that each weigh 11.5 g and measure 30.9–36.0 × 24.3–25.5 mm (Schönwetter 1967, Marantz et al. 2003). Based on the presence of brood patches in both sexes, Marantz et al. (2003) suggested that both sexes incubate and, probably, care for the young. In the present study, we contribute detailed information about timing of breeding, nest sites, parental care, and nestling development in the province of Misiones, Argentina, where White-throated Woodcreepers are common in primary and logged forests (Bodrati et al. 2010).

METHODS

Study Area and Field Methods.—Nests were found as part of a long-term study on the ecology of cavity-nesting birds (2006–2012, Cockle et al. 2012) or during general bird surveys (2003–2012). Each spring (Sep–Dec, the main breeding season for passerines in our study area), we searched for nests in primary forest, selectively

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logged forest, regenerating forest, and isolated trees on farms from San Pedro (26° 38′ S, 54° 07′ W) to Tobuna (26° 27′ S, 53° 54′ W), Misiones, Argentina. The study area is a mosaic landscape of small (2–100 ha) farms, nature parks and tree plantations, varying in elevation from 550–650 m. Natural forest remains in large blocks (>1,000 ha), fragments (0.5–50 ha), and corridors, and conforms to Cabrera's (1976) "mixed forest with laurel (*Nectandra* spp. and *Ocotea* spp.), guatambú (*Balfourodendron riedelianum*) and Paraná pine (*Araucaria angustifolia*)". To find nests, we walked along pre-established trails and roads, randomly-placed transects, and off-trail; followed adult birds; looked for birds entering or emerging from cavities; listened for nestlings begging; and monitored cavities that were used in previous years.

We also nailed 90 nest boxes to trees at heights of 6–10 m. Twenty-six boxes were placed in 90 ha of highly degraded forest at Parque Provincial de la Araucaria in 2006 and monitored through 2008; 30 boxes were placed in 2 ha of primary forest at Parque Provincial Cruce Caballero in 2007 and monitored through 2009; and 34 boxes were placed in 2.5 ha of selectively logged forest near Tobuna in 2007 and monitored through 2009 (Cockle and Bodrati 2009, Cockle et al. 2010). Each box had a round or diamond-shaped entrance 5–12 cm in diameter in the middle of the front panel. The boxes were 40–60 cm deep in Parque Provincial de la Araucaria and 60 cm deep in PP Cruce Caballero and Tobuna. We placed about 5 cm of sawdust in the bottom of each box to simulate the conditions of natural cavities.

Contents of cavities and nest boxes were monitored using a small color video camera mounted on a 15-m telescoping pole or carried up to the cavity using single-rope climbing. We checked cavities and nest boxes every 1–3 weeks when they had no evidence of nesting, every 1–14 days when they contained eggs or nestlings, and every 1–2 days during laying and around the expected hatch date. A nest was presumed to be depredated if all eggs were missing from the cavity or nestlings were missing before they were fully feathered on the head, back, and wings. We also watched nests from the ground using binoculars or a telescope for a total of 5 hrs during the courtship, nest-building, and laying period, 17 hrs during incubation, and 85 hrs during the nestling period to study adult behavior. We took the following measurements after the chicks had fledged: tree diameter at breast height (DBH), cavity height (from lower lip of lowest entrance to ground), vertical and horizontal diameter of each entrance to the cavity and cavity depth (from lower lip of lowest entrance to floor of cavity). Additionally, we report on two nesting attempts that we recorded during bird surveys in mixed forest with laurel and guatambú at Area Experimental Guaraní (26° 56′ S, 54° 13′ W, 400 m elevation) and Parque Provincial Moconá (27° 09′ S, 53° 54′ W, 250 m elevation), both in Yaboty Biosphere Reserve.

RESULTS

We recorded 16 nesting attempts of White-throated Woodcreepers at Parque Provincial Cruce Caballero, Tobuna, Area Experimental Guaraní, and Parque Provincial Moconá, in nine natural cavities and two nest boxes (Table 1).

Timing of Reproduction.—Adults were observed entering a cavity with bark as early as 18 September (nest 6) and eggs were observed as early as 22 September (nest 8). Hatch day was known for five nests, and varied from 6 October (nest 5) to 13 November (nest 9) with a median of 16 October (nest 11). The last nest, which was shared with a roosting female Helmeted Woodpecker (*Dryocopus galeatus*, see below), contained nearly-fledged nestlings on 2 December (nest 9).

Nest Site, Courtship, and Construction.—All nests were found in primary or selectively logged forest. None were in highly degraded forest, in isolated trees on farms, or in small (<10 ha) forest patches, although nest 4 was in a cavity that faced onto a 7-ha tobacco field surrounded by forest. All nine natural cavities used for nesting were created by damage (branch fall, fissure, etc.) and decay processes, in a live tree-trunk or a large live branch. White-throated Woodcreepers were not found nesting in cavities created by woodpeckers, nor in cavities in dead trees or dead branches. The natural cavities ranged in shape from round holes to long cracks, in size from 3.3–8.3 cm in diameter and 46–103 cm in depth, and in height from 3.0–16.9 m above the ground (mean ± SD = 9.0 ± 4.6, n = 9; Table 1). One of the adults (presumably the slightly larger female; Marantz et al. 2003) appeared to have trouble squeezing into the 3.3 cm wide cavity (nest 7).

Nest 11 was observed during the courtship period. Both adults slept in the cavity for at least two nights, 5 and 4 days before eggs were laid.

TABLE 1. Characteristics of cavities and nests of White-throated Woodcreepers (*Xiphocolaptes albicollis*) in Misiones, Argentina. Tree diameter was measured at breast height (DBH). Clutch size is given for clutches known to be complete.

			Nest tree		Cavity							
Nest ID	Locality[a]	Habitat	Species	DBH (cm)	Origin	Height above ground (m)	Diameter (vertical × horizontal; cm)	Depth (cm)	Year	Stage found[b]	Clutch size	Fate
1	Tobuna	Logged forest, 50 m from farm edge	*Myrciaria rivularis*	31	Decay	4.7	20 × 5	46	2007	I	3	Unknown
2			same cavity as above						2008	I	2	Fledged
3			same cavity as above						2009	E		Unknown
4	Tobuna	Logged forest edge, facing tobacco field	*Apuleia leiocarpa*	51	Decay	11.9	5.5 × 5.5	49	2010	E		Unknown
5	Cruce	Primary forest	*Myrocarpus frondosus*	68	Decay	16.9	12.9 × 7.7, 10.6 × 8.1	103	2008	H		Fledged
6	Cruce	Primary forest	*Alchornea triplinervia*	106	Decay	10.6	18.8 × 3.3	93	2007	C or E		Usurped
7	Cruce	Primary forest	Same cavity as above						2011	L	4	Fledged
8	Cruce	Primary forest	Same cavity as above						2012	L	3	Failed (tree fell)
9	Cruce	Primary forest	*Apuleia leiocarpa*	87	Decay	12.4	38 × 6	90	2010	I	3	Fledged
10	Cruce	Primary forest	*Ateleia glazioveana*	31	Decay	10.2	13 × 8.3	56	2010	N		Unknown
11	Cruce	Primary forest	Same cavity as above						2011	C	2	Depredated
12	Cruce	Primary forest	*Ruprechtia laxiflora*	29	Decay	3	29 × 6	54	2012	H		2 fledged, 1 died
13	Cruce	Primary forest			Nest box	8	12 × 10	60	2009	N		Unknown
14	Tobuna	Logged forest, 200 m from farm edge			Nest box	8	12 × 10	60	2007	E		Unknown
15	Moconá	Primary forest	*Peltophorum dubium*		Decay	~6			2005	C or E		Unknown
16	Guaraní	Lightly logged forest	*Enterolobium contortisiliquum*		Decay	5			2005	C or E		Unknown

[a] Cruce = Parque Provincial Cruce Caballero, Moconá = Parque Provincial Moconá, Guaraní = Area Experimental Guaraní.

[b] Stage of nest when found C = courtship, L = laying, I = incubation, E = egg (laying or incubation), H = hatching, N = nestling. 'C or E' indicates adults were seen entering the cavity with nesting material, but we did not inspect the cavity.

They arrived at the tree together without nest material, vocalized softly, and then entered the cavity, one right after the other, 8 and 14 minutes after sunset on the respective days. Both adults brought material to line the nesting cavity, including the bark of Paraná pine and a seed pod of angico colorado (*Parapiptadenia rigida*). Adults continued to bring material throughout laying and incubation. When the nestling period was over, the bottom of the cavity was lined with flakes of bark and a few leaf fragments.

Eggs.—Eggs (n = 25) were immaculate white. Complete clutches had 2–4 eggs (mode = 3, mean ± SD = 2.8 ± 0.75, n = 6; Table 1). Two cracked eggs, collected from nest 8 when the tree fell, measured 32.7 × 24.5 mm and 34.0 × 23.3 mm. Eggs were laid on alternate days. Adults did not roost in the nest between laying the first and second egg (nest 8).

Incubation.—The incubation period was 17 days at nest 11, and 17–19 days at nest 7. Both adults participated in incubation. They nearly always brought a piece of bark to the cavity when they arrived, and twice were seen to remove bark from the cavity when they left. One complete incubation bout lasted 1 hr 50 mins. Three incomplete incubation bouts lasted >2 hrs 9 mins, >2 hrs, and >1 hr 40 mins, respectively. Nest attentiveness during incubation was 93%, but incomplete incubation bouts resulted when adults left the nest unattended when interrupted by the observer (n = 2) or when interacting with another bird (n = 6). One adult roosted in the cavity every night of the incubation period.

Hatching and Nestling Development.—Broken egg shells were never observed in the nest. Nestlings hatched with pink skin, dark gray down, and yellowish gape flanges. By day 5, they had visible pin feathers and the eyes were opening. By day 7, feathers were emerging from pins and the bill was blackish. By day 8, we could hear them vocalizing "*uichu uichu*," a voice that recalled the adult song but was much more monotonous. By day 11, their eyes were fully open and feathers were visible on the bodies, wings, and tail. By day 13, they uttered a weak and high-pitched version of the adult song, switching to "*uichu uichu*" when the adults came to the nest. Adults sometimes responded to the "*uichu uichu*" call with a deeper note "*eee*." By day 15, the nestlings appeared well feathered with black and white streaking on the head, brown backs, and a black bill with yellow tip, but feathers did not emerge from pins on the tail until sometime after day 16. Subcutaneous botflies (*Philornis* spp.) were apparent in the faces of two nestlings at nest 12 beginning on day 5, and in at least one nestling at nest 11 beginning on day 7.

Nestling Diet and Parental Care.—Nestlings were fed a diet of arthropods (n = 158) and vertebrates (n = 3). Most of the items we could identify were insects (n = 86), in the orders Lepidoptera (14 adult butterflies and moths, 4 pupae, 19 larvae), Orthoptera (15 grasshoppers and crickets), Coleoptera (13 beetles), Hemiptera (4 cicadas and 1 other true bug), Odonata (1 dragonfly), Hymenoptera (1 wasp), Diptera (1 fly), and Blattaria (1 cockroach). The other arthropods were Arachnida (20 spiders, 2 harvestmen, and 1 scorpion), Chilopoda (3 centipedes) and Diplopoda (2 millipedes). The vertebrates were two frogs and a snake about 20 cm long. AB also observed fledglings being fed small unfeathered nestling birds, once at Parque Provincial Cruce Caballero and once at Estancia Quinto Potrero, Departamento Caaguazú, Paraguay (25° 14′ S, 56° 10′ W).

Food delivery rate ranged from 0.7 to 7.4 visits/hr (mean ± SE = 3.0 ± 0.24, n = 44), and there was no directional change in delivery rate over time (nestling day was not a significant predictor in either quadratic or linear mixed-effects models predicting feeding rate; a null model had lowest AIC_c). On days 0–2, most prey items were small and could not be identified, but by days 3 and 4, 40% of prey were as long as the adult's bill (~5 cm; n = 18 items for which size was recorded). Vertebrates appeared in the diet by day 9, and 56% of food items were as large as the adult's bill by days 12–19 (n = 45 items for which size was recorded). Occasionally, after arriving with a large prey item, the adult would emerge from the cavity still carrying the prey, then reenter and deliver the food item a few minutes later. Parents often reused the same trees to make their way to and from the nest. One member of the pair usually came from one direction and the other came from another part of the forest. Additionally, one member of the pair spent more time clinging to the tree before entering the cavity and sometimes flew away without entering if it detected an observer.

We did not observe adults removing fecal sacs during 13 hrs 37 mins of observation from hatch day to nestling day 2. We first observed adults removing fecal sacs on day 3, and thereafter the

rate of removal ranged from 0.5–3.8 trips/hr (mean ± SE = 0.80 ± 0.15, n = 36). We continued to observe this behavior until nestlings fledged (nest 12), with no significant change in removal rate over the nestling period (nestling day was not a significant predictor in either quadratic or linear mixed-effects models predicting log-transformed rate of fecal sac removal; a null model had lowest AIC_c). However, the adults did not enter the cavity to remove fecal sacs when they fed the older nestlings at the entrance (e.g., day 19 at nest 12). A smaller adult (presumed male) removed fecal sacs on 12 of 24 visits, significantly more than the larger adult (presumed female) which removed a fecal sac on only 1 of 21 visits (X^2 = 9.06, P = 0.0026; nests 7 and 12). One adult slept in the cavity with nestlings at least until day 17 at nest 9 and at least until day 11 at nest 12.

Fledging.—Fledging was observed only at nest 12. One chick fledged on day 19 and the other on day 20. Parents were still delivering food on day 19 at nest 9 when we left the study area. Adults delivered food on day 21 but not day 22 at nest 5. Nestlings were not found in the nest on day 18 at nest 7 and were presumed fledged. We thus calculate the nestling period as lasting 18–22 days.

On nestling day 19, when one nestling remained in nest 12, the adults called to the nestling when they came close to the nest with food. Both adults attended this nestling, and at least one attended the fledgling, which remained within 20 m of the nest tree and was fed twice in 2 hrs 10 mins. The second fledgling was clinging to the nest tree beside the cavity at 0630 Argentina Time on day 20. It vocalized softly, similar to the adult voice. It made its first short flight (about 6 m) 20 mins later when an adult arrived with food and vocalized softly from another tree. The fledgling was fed then and again 25 mins later in the same spot. Both fledglings looked like adults but with shorter tails and whitish-yellow gape flanges.

Nest Fate.—Five nests were found before eggs hatched and had a known fate. Three of these fledged, one was depredated, and the other failed when the tree fell during a storm, breaking the eggs (Table 1). Successful nests (n = 5) fledged 2 or 3 nestlings (mean ± SE: 2.4 ± 0.24). Of the two nests infested with botflies, one failed completely to predation (nest 11) and the other fledged two of the three chicks (nest 12). One of the nestlings at nest 12 died in the cavity sometime after day 11. It was found dead on day 15 with unopened pin feathers in the tail, a naked belly, and yellowish feathering on the sides and breast. The cavity smelled foul. The dead nestling was gone from the nest by day 16.

Interactions with Other Birds.—Adults did not chase away a Red-rumped Cacique (*Cacicus haemorrhous*) less than 1 m from their nest hole or a Pileated Parrot (*Pionopsitta pileata*) about 2.5 m away. However, they chased away a White-eyed Parakeet (*Aratinga leucophthalma*) that tried to enter the nesting cavity, and a Planalto Woodcreeper (*Dendrocolaptes platyrostris*), and another White-throated Woodcreeper that came close to the cavity. Plush-crested Jays (*Cyanocorax chrysops*) were twice chased away but other times the White-throated Woodcreepers tolerated them near the nest. The pair at nest 9 shared their cavity with a female Helmeted Woodpecker, which roosted in the upper part of the cavity throughout their incubation period. The Helmeted Woodpecker had roosted in this cavity on several occasions before the White-throated Woodcreepers arrived, including two nights sharing the cavity with a pair of White-eyed Parakeets (Cockle 2010, Lammertink et al. 2012). During the time that the two species shared the cavity, we watched it during four mornings and four evenings, with fights arising on four of these eight occasions, though both species always ended up occupying the cavity. When the White-throated Woodcreeper chicks were 2–3 days old, the Helmeted Woodpecker stopped coming to the cavity.

Cavity Reuse.—We recorded White-throated Woodcreepers reusing three of the nesting cavities in subsequent years (Table 1). At least seven of the cavities were also used for 16 nesting attempts by five other species of birds: Maroon-bellied Parakeet (*Pyrrhura frontalis*), White-eyed Parakeet, Ferruginous Pygmy-Owl (*Glaucidium brasilianum*), Chestnut-eared Aracari (*Pteroglossus castanotis*) and Planalto Woodcreeper.

DISCUSSION

Nesting of the White-throated Woodcreeper was in many respects similar to that of other woodcreepers, in particular *Xiphocolaptes*. Like other woodcreepers, the parents brought nesting material throughout the incubation period, removed eggshells and other refuse from the nest immediately, and ate or removed fecal sacs until fledging (Skutch 1969, Cockle and Bodrati 2009,

Bodrati and Cockle 2011). The clutch size and incubation period were similar to those of the larger Great Rufous Woodcreeper at similar latitudes in Argentina, but the nestling period was shorter (Bodrati 2003, Di Giacomo 2005; AB, pers. obs.; Table 2). Like other woodcreepers, White-throated Woodcreepers hatched with pink skin, gray down, and yellowish gape-flanges (Skutch 1969, Marantz et al. 2003, Cockle and Bodrati 2009, Bodrati and Cockle 2011). White-throated Woodcreeper nestlings in at least two nests were infested with botfly larvae, as were some Great Rufous Woodcreeper nestlings in Parque Nacional Chaco and Parque Provincial Pampa del Indio and 97% of Planalto Woodcreeper nestlings in our study area in Misiones (Cockle and Bodrati 2009, Norris et al. 2010; AB, pers. obs.).

The nine natural cavities occupied by White-throated Woodcreepers in the present study averaged 9 m above ground, quite high for woodcreepers. Marantz et al. (2003) reported that most woodcreeper nests have been found close to the ground; however, they also noted this may be a sampling artifact. In our study area, average nest height was 2.2 m for Scalloped Woodcreepers (*Lepidocolaptes falcinellus*, $n = 2$), 11 m for Planalto Woodcreepers ($n = 11$), 13 m for Olivaceous Woodcreepers (*Sittasomus griseicapillus*, $n = 2$), and 13 m for cavity-nesting birds overall ($n = 151$; Bodrati and Cockle 2011, Cockle et al. 2011b, Bodrati et al. 2012; KC, unpubl. data). In contrast, in the Chaco where forest canopy is considerably lower, most cavities of Great Rufous Woodcreepers were 2–7 m high (Bodrati 2003, Di Giacomo 2005; AB, pers. obs.). Nests of woodcreepers may thus be quite high above the ground in subtropical humid forest, and like other cavity-nesters, some woodcreepers may select higher cavities to avoid predation by terrestrial predators (Cockle et al. 2011b).

Like other large-bodied cavity nesters in our study area, White-throated Woodcreepers selected deep cavities (Cockle et al. 2011b). Similarly, Great Rufous Woodcreepers used cavities 45–70 cm deep in the Chaco (Bodrati 2003, Di Giacomo 2005; AB, pers. obs.). All nine natural cavities used by White-throated Woodcreepers in the present study were generated by decay processes (non-excavated cavities); in contrast, 5 of 13 Great Rufous Woodcreeper cavities in the Chaco and 1 of 11 Planalto Woodcreeper cavities in Misiones were old woodpecker holes (Bodrati 2003, Cockle et al. 2012; AB, pers. obs.; KC, unpubl. data). Woodpecker holes constitute about 20% of available cavities in our study area, but they collapse after an average of 2 yrs (Cockle et al. 2011a). Additionally, of 51 woodpecker holes used by cavity-nesting birds in our study area, only 4 were more than 45 cm deep, suggesting that most woodpecker holes are not deep enough for the White-throated Woodcreeper (KC, unpubl. data). Unlike the Planalto Woodcreeper, we found no nests of White-throated Woodcreeper in highly degraded forest (Parque Provincial de la Araucaria), small (<10 ha) forest patches or isolated trees on farms, despite the availability of suitable nest-boxes in the former two habitats. We surmise that White-throated Woodcreepers are more selective about breeding habitat and less tolerant of anthropogenic disturbance.

Three cavities were used for more than one nesting attempt of the White-throated Woodcreeper, but never more than three times over the 7 year study period, although other species of birds used the cavities on several occasions. In contrast, Great Rufous Woodcreepers used the same cavity in a Brazilian orchid tree, "pata de

TABLE 2. Breeding biology of *Xiphocolaptes* woodcreepers.

Species	Clutch size	Incubation period (days)	Length of incubation on-bouts	Nestling period (days)	Parental care	Sources
Strong-billed Woodcreeper	2–3	Unknown	Unknown	21–24 (estimated)	Biparental	Botero-Delgadillo and Olaciregui 2011
Moustached Woodcreeper	Unknown	Unknown	Unknown	Unknown	Unknown	
White-throated Woodcreeper	2–4	17	2 hrs	18–22	Biparental	This study
Great Rufous Woodcreeper	2–3	16–18	Unknown	24–27	Biparental	Bodrati 2003, Di Giacomo 2005; AB, pers. obs.

vaca'' (*Bauhinia forficata*) in Parque Nacional Chaco during 7 successive years from 1997–2003 (AB, pers. obs.). Since the birds were unmarked, we could not determine whether they were the same individuals. With so many similar-sized cavity-nesting species in the Atlantic forest, there may be few possibilities for a White-throated Woodcreeper to reuse a nest-site over many years.

Our results confirm that both male and female White-throated Woodcreepers build nests, incubate eggs, and care for nestlings, but suggest that their relative contribution may not be equal. The Great Rufous Woodcreeper, the *Dendrocolaptes*, the *Dendroplex*, and the *Lepidocolaptes* also exhibit biparental care, in contrast to the *Dendrocincla*, *Xiphorhynchus*, and *Sittasomus* (Skutch 1967, 1996; Marantz et al. 2003; Bodrati and Cockle 2011; Bodrati et al. 2012; Majewska and Oteyza 2013).

White-throated Woodcreepers' incubation onbouts lasted approximately 2 hrs. Incubation bouts have been reported for only nine other species of woodcreepers, none of them in the genus *Xiphocolaptes* (Majewska and Oteyza 2013, Table 2). The longest bouts reported were those of the White-throated Woodcreeper (this study) and the Planalto Woodcreeper (2 hrs 30 mins; Cockle and Bodrati 2009), in the same study area.

Food delivery rate has not been studied for other *Xiphocolaptes*. Parent White-throated Woodcreepers delivered food to nestlings at a rate of three visits per hour, a lower rate than that of the Planalto Woodcreepers, Scalloped Woodcreepers, and Olivaceous Woodcreepers in the same study area (Cockle and Bodrati 2009, Bodrati and Cockle 2011, Bodrati et al. 2012). Unlike Olivaceous Woodcreepers, parent White-throated Woodcreepers did not increase the rate of food delivery as the nestling period progressed (Bodrati et al. 2012). Adult White-throated Woodcreepers did not enter the cavity to remove fecal sacs when they fed the nestlings at the entrance, consistent with our observations of Great Rufous Woodcreepers (AB, pers. obs.).

We observed a pair of White-throated Woodcreepers roosting in their nest cavity prior to egg-laying, the first such observation made of any woodcreeper. Outside the breeding season, we have observed White-throated Woodcreepers roosting individually in tree cavities, but never as a pair, and not in old nest cavities (AB, pers. obs.). During the incubation and nestling periods, only one adult roosted in the nest. Roosting as a pair in the cavity prior to egg-laying could be a behavior related to courtship, copulation, or perhaps nest-site defense. Although Willis (1972) reported that promiscuous Plain-brown Woodcreepers (*Dendrocincla fuliginosa*) copulate vertically on tree trunks, we have not observed copulation in any socially monogamous woodcreeper and suggest that adult White-throated Woodcreepers might copulate inside their nest, like another Furnariid, the Brown Cacholote (*Pseudoseisura lophotes*; Nores and Nores 1994). In agreement with Skutch (1969), we have never observed any other incidents of woodcreepers returning to their old nest cavities to roost.

Basic studies of woodcreeper nesting biology should soon enable researchers to perform in-depth comparisons of the life history, behavior, and nesting niche of this interesting group of birds, to test ecological theory. Future research should address life history evolution and niche partitioning in the woodcreeper radiation. In particular, we recommend studies of marked individuals to confirm male and female contributions to incubation, provisioning, nest defense and nest hygiene. Such studies would also confirm whether the two members of a pair use different foraging areas, as suggested by our observations of White-throated and Great Rufous woodcreepers (AB, pers. obs.).

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TEMPORAL AND ENVIRONMENTAL EFFECTS ON THE BEHAVIOR OF FLIGHTLESS CORMORANTS

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ABSTRACT.—Flightless Cormorants (*Phalacrocorax harrisi*), the only flightless members of their 27-member genus, are listed as vulnerable on the International Union for Conservation of Nature (IUCN) Red List. The world population of <1,000 breeding pairs is restricted to scattered small colonies along the coastlines of Isla Fernandina and Isla Isabela, Galápagos, Ecuador. No previous study has systematically examined daily activity patterns by these birds in relation to environmental variables. We made half-hourly behavior scan counts at a colony of Flightless Cormorants at Cabo Douglas, Isla Fernandina during the daylight hours of 7 consecutive days in May 2011. We used generalized linear models and multi-model inference to examine the response of colony occupancy and behaviors to hour of day, height of tide, temperature, humidity, wind speed, barometric pressure, solar elevation, and solar flux. We show that the behavior of Flightless Cormorants during our period of study was shaped primarily by time of day, wind speed, and solar flux; unlike many marine birds, they responded little to tide. *Received 29 October 2012. Accepted 14 June 2013.*

Key words: diurnal activity, environmental factors, Flightless Cormorants, Galápagos Islands, generalized linear models, multi-model inference, *Phalacrocorax harrisi*.

Flightless Cormorants (*Phalacrocorax harrisi*), first discovered by the 1897–1898 Webster-Harris expedition (Rothschild and Hartert 1899), are large, conspicuous birds oddly overlooked by many earlier nineteenth-century expeditions to the Galápagos Islands, Ecuador (Livezey 1992). The world population of fewer than 1,000 breeding pairs (Valle and Coulter 1987, Livezey 1992, Jiménez-Uzcátegui and Vargas 2007) is restricted to small colonies scattered along <400 km of the coastlines of Isla Fernandina and Isla Isabela, Galápagos (Harris 1974, Rosenberg et al. 1990). Flightless Cormorants exhibit more than twice the mass of other cormorants (Wilson et al. 2008), and they are the only flightless and sequentially polyandrous members of their 27-member genus (Livezey 1992, Johnsgard 1993, Valle 1994, Kennedy et al. 2009). They are relatively long-lived; Jiménez-Uzcátegui et al. (2012) reported capture of a female Flightless Cormorant at least 17 years old, the oldest recorded age for any member of this species. Mitochondrial DNA analysis indicates that Flightless Cormorants are closely related to Double-crested Cormorants (*P. auritus*) and Neotropic Cormorants (*P. brasilianus*; Kennedy et al. 2009). Unlike their abundant mainland congeners, however, Flightless Cormorants are listed as vulnerable on the International Union for Conservation of Nature (IUCN) Red List (IUCN 2012).

Rothschild (1898) provided the first brief description of Flightless Cormorants, referring to the discovery of these birds as "the most remarkable" of the Webster-Harris expedition. Since then, a modest number of studies have characterized aspects of their morphology, behavior, population patterns, recovery from El Niño events, and breeding strategies (Rothschild and Hartert 1899, 1902; Snodgrass and Heller 1904; Townsend 1929; Davis 1938; Snow 1966; Harris 1974, 1979; Hennemann 1984; Tindle 1984; Valle and Coulter 1987; Rosenberg et al. 1990; Livezey 1992; Valle 1994, 1995; Jiménez-Uzcátegui and Vargas 2007). Recent studies have focused on factors that influence the viability of Flightless Cormorants in face of environmental change. Travis et al. (2006), for example, found these birds to be seronegative to a wide variety of avian pathogens and suggested they may have a reduced capacity to cope with introduced pathogens. Wilson et al. (2008) examined the energetics of diving behavior in Flightless Cormorants and opined that this species will be unable to accommodate to significant, long-term environmental change. Duffie et al. (2009) demonstrated the

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existence of significantly lower genetic diversity in these birds than among four other more widely distributed congeners, a result reinforcing the view that this endemic Galápagos species is particularly vulnerable to environmental change.

Hennemann (1984) reported time budgets for a group of 15–20 Flightless Cormorants on Isla Isabela. Except for behaviors associated with thermoregulation, however, he did not relate time budget data to temporal or environmental variables. Indeed, no previous study has systematically examined daily activity patterns of Flightless Cormorants in relation to environmental variables. In view of global warming and other environmental change, baseline profiles of behavior in relation to environmental variables are crucial for proper management of this vulnerable species.

Our study involved half-hourly occupancy and behavior scan counts at a colony of ~35 Flightless Cormorants at Cabo Douglas, Isla Fernandina in May 2011, toward the beginning of the period of heightened breeding activity (Harris 1979) and during a La Niña year of cooler than average sea surface temperatures (SST). We use generalized linear models and multi-model inference to test the following hypotheses: 1) the number of cormorants on land is related to environmental variables; 2) thermal stress influences the incidence of preening, wing spreading, rest posture, back sleep, and gular flutter; and 3) thermal stress inhibits the performance of courtship behavior.

METHODS

Data Collection.—Half-hourly counts of all Flightless Cormorants visible from a vantage point adjacent to Sea Lion Bay, Cabo Douglas (0° 18′ 13″ S, 91° 39′ 8″ W), Isla Fernandina, Galápagos were made during the daylight hours, from 1000–1800 Galápagos Time (GALT) on 10 May, from 0600–1800 on 11–16 May, and from 0600–1000 on 17 May 2011. The 176 half-hourly counts ranged from 11–35 birds. Each bird was tallied as occupying land or water. Each bird on land was tallied as occupying one of the following behavior states: preen (drawing feathers through the bill, scratching, shaking), wings spread, rest posture (standing or sitting without other activity), back sleep (head and neck turned back with bill tucked beneath scapulars [Amlaner and McFarland 1981, Amlaner and Ball 1983, Shaffery et al. 1985]), or courtship (snake-necking, nuptial dancing, copulation [Snow 1966]). Additionally, birds with wings spread or in a rest posture engaged in gular flutter were noted. On each morning of 11, 12, and 15 May, we recorded the time at which the first cormorant entered the water.

TABLE 1. Means (± SD) and ranges of environmental variables during 7 days of data collection on the behavior or Flightless Cormorants at Cabo Douglas, Isla Fernandina, Galapagos, 10–17 May 2011.

Environmental variable	Mean ± SD	Range
Tide height (m)	1.0 ± 0.4	0.2–1.8
Ambient temperature (°C)	27.4 ± 2.0	21.6–31.1
Relative humidity (%)	75.1 ± 8.5	55–96
Wind speed (m/sec)	14.2 ± 7.0	0–25.7
Barometric pressure (mmHg)	757.7 ± 1.4	754.4–760.0
Solar elevation (°)	39.2 ± 23.2	−0.1–72.62
Solar flux (W/m^2)	486.0 ± 296.5	15–1,132

Concurrent with scan counts, a Vantage Vue® wireless weather station (Davis Instruments Corp. Hayward, California, USA), mounted 1.8 m above site elevation on a white sandy beach at Cabo Douglas logged wind speed, barometric pressure, ambient temperature, and relative humidity. Solar elevation was obtained from an online calculator provided by the National Oceanic and Atmospheric Administration (Cornwall et al. 2013) Tide height was determined with a 4-m surveyor leveling rod erected in small bay largely protected from wave action.

Solar flux was recorded at half-hourly intervals using a hand-held TM-206 Solar Power Meter (Ambient Weather Corp., Chandler, Arizona, USA) from 1000–1730 on 10 May, and from 0700–1730 on 11–16 May in conjunction with a different project at the same site (Payne 2012). Thus, we obtained solar flux data for a subset (n = 148) of the 176 scan counts. Table 1 presents averages and ranges of environmental conditions for the hours of data collection.

Smoothing of Tide Height Observations.—Although the tide pole was protected from major wave action and the observed water levels showed a clear tidal dynamic, they were nevertheless noisy. To increase accuracy we smoothed the tide data as follows. For each day of observations, we fitted a smooth curve through the observed tide heights using the Lowess smoothing function in Axum with 10 iterations, 25% points for each local regression, and 100 output points (Axum 6.0 1999). In MATLAB® (MATLAB® 2012), we splined the 100-point output from the Lowess

smoothing routine and obtained interpolated tide heights at 30-min intervals.

Analysis.—We used generalized linear models (McCullagh and Nelder 1989) with multi-model inference based on the AIC_c (Burnham and Anderson 2002) to study the relationship of occupancy counts and on-land behaviors to the environmental factors *TIME* (hour of day), *TIDE* (tide height in m), *TEMP* (ambient temperature in degrees Celsius), *HUM* (relative humidity as a percent), *WIND* (wind speed in m/sec), *BAR* (barometric pressure in mmHg), *SOLEL* (solar elevation in degrees above of the horizon), and *SOLF* (solar flux in W/m^2). First we analyzed the subset of data for which we had *SOLF* values ($n = 148$). Then, for those dependent variables for which *SOLF* was discarded as a factor, we analyzed the complete data set ($n = 176$) with the remaining seven factors.

For land occupancy counts, we used the global Poisson regression model (with intercept, without interactions) together with all of its submodels as the basis for multi-model inference. For behavior incidence, we took the same approach except we used logistic regression, with occupancy as the number of trials. We used the package glmulti (Calcagno 2012) in the statistical computing environment R (R Development Core Team 2012) to compute model-averaged parameter estimates and relative factor importance based on Akaike weights (Burnham and Anderson 2002).

Because the small data sets led to uncertainty in model selection, we did not choose "best" models. For each model-averaged coefficient β having a completely positive or completely negative confidence interval, we computed the count ratio (for occupancy) or odds ratio (for behaviors) as $\exp(c\beta)$ (Hosmer and Lemeshow 2000). This is the multiplier by which the count, or odds, changes with a c-unit increase in the corresponding factor if all other factors are held constant.

Counts of cormorants in the water were difficult to make for three reasons: 1) foraging sometimes occurred behind a large rock outcrop that blocked our view, 2) birds underwater during a dive were not counted, and 3) wave action sometimes obscured swimming birds (see also Hennemann 1984). Consequently, we did not include counts of cormorants in the water as part of our regression analyses. We present counts of cormorants in the water summed by count period over the 7-day study.

RESULTS

Of the eight environmental variables measured, only four—time of day, solar flux, wind speed, and barometric pressure—influenced the monitored behavior states and land occupancy of Flightless Cormorants. Solar elevation, ambient temperature, relative humidity, and tide height were unimportant (Tables 2 and 3).

Hypothesis 1: The Number of Cormorants on Land is Related to Environmental Variables.—Regression showed that if all other factors were held constant, land occupancy increased 11% with a 3-hr increase in time of day (Table 2 and Fig. 1A). Thus, our hypothesis is supported for time of day, but not for variables of weather and tide.

Cormorants not on land presumably were in the water, although topography, water conditions, and birds engaged in diving during our counts interfered with our capacity to count all birds in the water. The average number of cormorants observed in the water during any hour of the day was variable but generally low (Fig. 1B). On 11, 12, and 15 May, times for the first cormorant of the day to enter the water were 0551, 0557, and 0555, respectively, or just prior to dawn. Between 0800–0900, there was an increase in the average number of birds in the water, followed by a decline toward dusk, although counts were low and count variability was high. During and following our last 1800-hr count, we never observed cormorants in the water. During moonlit nights and during the 2 hrs before sunrise, virtually all individuals were in a back sleep posture on land.

Hypothesis 2: Thermal Stress Influences the Incidence of Preening, Wing Spreading, Rest Posture, Back Sleep, and Gular Flutter.—Our hypothesis is partially supported. If all other factors were held constant, the odds of gular flutter increased 51% with a 200 W/m^2 increase in solar flux, increased 105% for a 3-hr increase in time of day, and increased 106% for a 3 mmHg rise in barometric pressure.

Individuals that engaged in gular flutter, an indicator of thermal stress, could not simultaneously engage in back sleep or preen. The odds of back sleep decreased 28% with a 200 W/m^2 increase in solar flux, although the incidence of preen was unaffected by solar flux. In addition, a 10 m/sec increase in wind speed increased the odds of back sleep by 48%, but decreased the odds of preening by 23% (Table 2), and decreased the odds of gular flutter by 48% (Table 3).

TABLE 2. Responses of colony occupancy, preen, wings-spread, and courtship behavior by Flightless Cormorants to seven environmental factors, with factor importance and model-averaged coefficient estimates β. Positive (or negative) coefficients correspond to an increase (or decrease) in the response variable given an increase in the factor. Confidence intervals that are completely positive or negative indicate significance at the $\alpha = 0.05$ level. For a given c-unit increase in a significant factor, $e^{\beta c}$ is the count ratio for occupancy and the odds ratio (OR) for behaviors. The percent change in occupancy or odds of a behavior is the difference between $e^{\beta c}$ and *1*. Asterisks (*) identify significant factors (confidence intervals that are completely positive or negative).

Response category	Factor	Importance	Coefficient β	95% confidence interval	c	$e^{\beta c}$	%Δ
Colony occupancy	(Intercept)	1	1.8103	(−9.2443, 12.87)			
	*TIME**	1.0	0.03557	(0.02099, 0.05015)	3 hrs	1.11	11% ↑
	TEMP	0.71	−0.02945	(−0.08511, 0.02621)			
	HUM	0.45	−0.002447	(−0.01112, 0.006221)			
	SOLEL	0.42	0.0005458	(−0.001316, 0.002407)			
	TIDE	0.38	0.01759	(−0.04400, 0.07919)			
	WIND	0.29	−0.0003617	(−0.003160, 0.002436)			
	BAR	0.28	0.002413	(−0.01181, 0.01663)			
Preen	(Intercept)	1	4.318	(−22.37, 31.00)			
	*WIND**	1.0	−0.02638	(−0.04132, −0.01144)	10 m/sec	0.77	23% ↓
	SOLEL	0.74	0.002989	(−0.001775, 0.007754)			
	TIME	0.68	0.01840	(−0.01568, 0.05248)			
	TEMP	0.38	0.01208	(−0.03777, 0.06194)			
	BAR	0.32	−0.007415	(−0.04232, 0.02749)			
	HUM	0.31	−0.001025	(−0.007404, 0.005354)			
	TIDE	0.28	0.0002704	(−0.05543, 0.05597)			
Wings-spread	(Intercept)	1	−53.51	(−155.7, 48.67)			
	BAR	0.64	0.06529	(−0.06820, 0.1988)			
	SOLEL	0.59	0.003400	(−0.004165, 0.01097)			
	TEMP	0.59	0.05962	(−0.07539, 0.1946)			
	WIND	0.59	−0.01189	(−0.03854, 0.01476)			
	TIME	0.42	0.01327	(−0.02979, 0.056320)			
	HUM	0.33	−0.0001343	(−0.01076, 0.01049)			
	TIDE	0.29	0.01947	(−0.1009, 0.1399)			
Courtship	(Intercept)	1	22.58	(−61.48, 106.6)			
	*TIME**	1.0	−0.2031	(−0.2849, −0.1213)	3 hrs	0.54	46% ↓
	TIDE	0.73	−0.3411	(−0.9043, 0.2221)			
	TEMP	0.59	−0.08050	(−0.2638, 0.1028)			
	HUM	0.37	0.002039	(−0.01966, 0.02374)			
	BAR	0.34	−0.02812	(−0.1378, 0.08153)			
	SOLEL	0.34	0.001207	(−0.005346, 0.007760)			
	WIND	0.31	0.003631	(−0.01423, 0.02150)			

Gular flutter occurred simultaneously with wings spread and rest posture. The odds of rest posture increased 12% with a 200 W/m^2 increase in solar flux, but the odds of wings spread were unaffected by any measured environmental variable.

Hypothesis 3: Thermal Stress Inhibits the Performance of Courtship Behavior.—The odds of courtship behaviors decreased 46% with a 3-hr increase in time of day, but no other environmental variable, including solar flux, was associated with the odds of courtship. Thus, our hypothesis was not supported.

DISCUSSION

Two special factors, one inherited and the other environmental, constrain the behavior of Flightless Cormorants. First, flightlessness, behavioral philopatry, or both reduces the home range of these birds (Wilson et al. 2008); indeed, a high degree of genetic differentiation among colonies has been demonstrated (Duffie et al. 2009). It has been noted, however, that these birds sometimes swim long distances along the coast (Valle 1995, Duffie et al. 2009). Second, prey abundance in the Galápagos varies dramatically and erratically with the occurrence of local upwellings (Boersma 1978, Valle

TABLE 3. Response of rest posture, back sleep, and gular flutter by Flightless Cormorants to eight environmental factors, with factor importance and model-averaged coefficient estimates β. Positive (or negative) coefficients correspond to an increase (or decrease) in the response variable given an increase in the factor. Confidence intervals that are completely positive or negative indicate significance at the $\alpha = 0.05$ level. For a given c-unit increase in a significant factor, $e^{\beta c}$ is the odds ratio (OR) of the behavior. The percent change in odds of the behavior is the difference between $e^{\beta c}$ and 1. Asterisks (*) identify significant factors (confidence intervals that are completely positive or negative).

Response category	Factor	Importance	Coefficient β	95% confidence interval	c	$e^{\beta c}$	%Δ
Rest posture	(Intercept)	1	−28.94	(−100.5, 42.65)			
	*SOLF**	1.0	0.0005524	(0.0001928, 0.0009121)	200 W/m^2	1.12	12% ↑
	TIME	0.82	0.03382	(−0.01234, 0.07998)			
	BAR	0.51	0.03597	(−0.05798, 0.1299)			
	TIDE	0.48	−0.07094	(−0.2654, 0.1235)			
	SOLEL	0.39	−0.001286	(−0.005771, 0.003199)			
	TEMP	0.34	0.01121	(−0.03353, 0.05595)			
	WIND	0.32	0.001837	(−0.006108, 0.009783)			
	HUM	0.27	−0.0002678	(−0.004982, 0.004446)			
Back sleep	(Intercept)	1	−1.194	(−33.54, 31.15)			
	*SOLF**	1.0	−0.001668	(−0.002256, −0.001081)	200 W/m^2	0.72	28% ↓
	*WIND**	0.99	0.03930	(0.01275, 0.06584)	10 m/sec	1.48	48% ↑
	TIDE	0.75	0.2438	(−0.1379, 0.6254)			
	HUM	0.66	−0.02114	(−0.06355, 0.02127)			
	TEMP	0.63	−0.1071	(−0.3359, 0.1217)			
	SOLEL	0.33	0.001224	(−0.003971, 0.006420)			
	TIME	0.33	−0.006751	(−0.03389, 0.02039)			
	BAR	0.28	0.004938	(−0.03534, 0.04522)			
Gular flutter	(Intercept)	1	−189.2	(−367.8, −10.57)			
	*WIND**	1.0	−0.06590	(−0.09721, −0.03459)	10 m/sec	0.52	48% ↓
	*SOLF**	1.0	0.002068	(0.001109, 0.003026)	200 W/m^2	1.51	51% ↑
	*TIME**	1.0	0.2391	(0.1113, 0.3669)	3 hrs	2.05	105% ↑
	*BAR**	0.91	0.2405	(0.006625, 0.4744)	3 mmHg	2.06	106% ↑
	SOLEL	0.55	0.006887	(−0.009748, 0.02352)			
	TEMP	0.40	0.03927	(−0.09488, 0.1734)			
	HUM	0.35	−0.004529	(−0.02364, 0.01459)			
	TIDE	0.29	0.03643	(−0.1624, 0.2353)			

1994). High levels of mortality and negligible reproductive output occur during El Niño events (Boersma 1978, Valle and Coulter 1987). How individual cormorants parse their time in relation to these factors and to a variety of other environmental variables contributes to their levels of fitness.

Our study occurred toward the beginning of the most active period of breeding (Apr–Oct), although breeding may occur in every month of the year (Harris 1979). The activity patterns we report must be evaluated in this context. Prolonged courtship activity, especially in the morning, was common both in and out of the water (Table 2). Groups of four birds frequently moved from place to place, on land and in water, snake-necking, walking, and swimming together (for detailed information on breeding behavior and timing, see Snow [1966], Harris [1979], Tindle [1984], and Valle [1994]). We noted five active nests in the colony. All nests were located on lava outcrops bordering the west side of Sea Lion Bay. Four of these nests were in early stages of construction, with the males repeatedly bringing algae to the females who did most of the nest arranging (Snow 1966). The remaining nest contained three eggs on 5 May, all of which disappeared after several days. We do not know the cause of the disappearance; we never observed predation attempts on the nest by any organism. Birds not engaged in breeding activity fed in the water and rested, preened, or slept on land.

Preening was one of the most common activities of Flightless Cormorants on land. This result comports with time budget data reported by Hennemann (1984) who found that birds off the nest but on land spent 49.9% of their time preening. In our study, the odds of preening decreased with increases in wind speed, a finding consistent with that for gulls (Henson et al. 2007, 2012). Preening is risky for birds

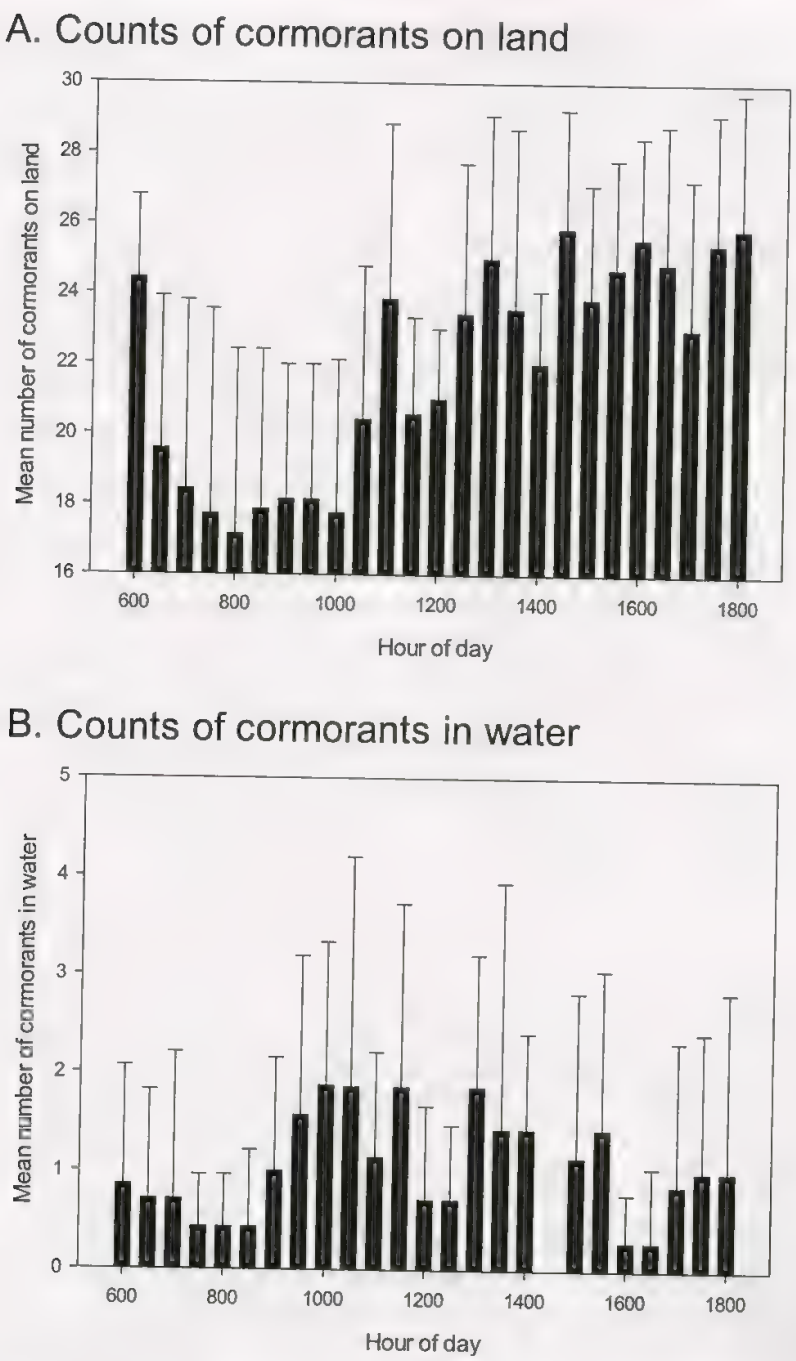

FIG. 1. Mean number of cormorants on land and in the water during half-hourly counts, 0600–1800 GALT, 10 May–17 May 2011, Cabo Douglas, Isla Fernandina, Galápagos. Error bars are standard deviations.

under conditions of high wind which can knock them off their feet. Back sleep posture, favored under these conditions, minimizes the surface area exposed to wind and thereby increases stability.

Wing spreading did not correlate with solar flux (Table 2). This result corroborates earlier findings with Flightless Cormorants, Double-crested Cormorants (Hennemann 1984), Little Cormorants (*Microcarbo niger*, Winkler 1983) and Great

Cormorants (*P. carbo*, Sellers 1995) that wing spreading is not for thermoregulation but functions to dry feathers.

Decreasing solar flux and increasing wind speed increased the odds of back sleep, a posture that minimizes heat loss by reducing the surface-to-volume ratio (Amlaner and Ball 1983, Reebs 1986). Increasing solar flux decreased the odds of back sleep but increased the odds of rest (Table 3); birds in rest can engage in gular flutter, which is crucial for unloading heat at higher temperatures (Bartholomew et al. 1968). The odds of gular flutter increased with solar flux, hour of day, and barometric pressure, and decreased with increasing wind speed. Birds using gular flutter cannot engage in sleep, preen, or courtship behavior, all of which promote fitness. Excessive gular flutter during El Niño events or global warming might interfere with physiological requirements and reduce reproductive output. The reproductive capacity of Flightless Cormorants fosters rapid population recovery following declines associated with El Niño events (Valle and Coulter 1987). Long-term global warming, however, may pose a more serious threat for these birds, given that flightlessness and the small size of the Galápagos Islands will not allow for the types of range shifts possible for other birds that seek to escape worsening conditions (Grémillet and Boulinier 2009).

Occupancy and all behaviors except gular flutter were associated with just one or two environmental factors. In contrast, gular flutter was associated with wind speed, solar flux, time of day, and barometric pressure, suggesting that these factors are involved in the Flightless Cormorants' heat index function, the form of which is currently unknown for these birds. Heat index functions indicate how thermal stress in an organism is related to the environment. They are species-specific and typically are determined experimentally in the laboratory. Of particular interest in such a function is the upper critical temperature of the thermoneutral zone at which the organism must begin to expend significant energy to unload heat (Porter and Kearney 2009). Heat storage and subsequent radiation by the dark lava rocks on which these birds spend much of their time undoubtedly played an important role in gular flutter, as evidenced by the importance of time of day independent of solar flux. Moreover, although our data on these birds in the water are limited, Figure 1B suggests there may be a tendency to offload heat during the afternoon in the water when thermal conditions on land are most stressful. We did not specifically observe birds drinking seawater when thermally stressed, although they probably did so while they were in the water. In view of the threat of dramatic declines in Flightless Cormorant numbers and reproductive output following El Niño events (Harris 1979, Valle and Coulter 1987) and of the concomitant threat of global warming to the long-range survival of this species (Edgar et al. 2010, Alava and Haase 2011), further study of the effects of heat stress on these birds is warranted.

Swimming birds foraged, displayed and courted, gathered algae for nest material, and fed juveniles, apparently hatched during the previous fall. Foraging seemed to occur throughout the day. According to Tindle (1984), foraging occupies about 4 hrs of the day in both males and females, and juveniles are fed by adult males for 5–9 months. Although we did not measure foraging durations nor did we know the ages of the juveniles, Tindle's estimates are consistent with our subjective impressions. The observation by Snow (1966) that juveniles leave their place on the rocks and swim out to meet and beg food from parents also comports with our observations.

Our results suggest that tide height, which influences the behavior of many marine organisms (Henson et al. 2004, Hayward et al. 2009), including some cormorants (van Tets 1965, Richner 1995, Anderson et al. 2004, Zeenath and Zacharias 2010), plays little role in the timing of behavior in Flightless Cormorants (Tables 2 and 3). Although tide height is highly correlated with time of day and to some degree with weather variables, our regression analysis held each of these latter factors constant when testing for the effects of tide; thus, we are confident that weak influence of tide on these birds is real. Moreover, tidal range was modest at Cabo Douglas during our study (1.6 m, Table 1), and Flightless Cormorants have the ability to dive to depths of up to 73 m for exceptionally long time periods (Wilson et al. 2008); thus the changes in tide height may have been relatively inconsequential for successful foraging in these usually (except during El Niño events) food-rich waters (Boersma 1978, Tindle 1984). Rather than shape their activity cycle around tides, an obvious advantage for intertidal and surface feeders such as gulls (Henson et al. 2004, Hayward et al. 2009), these equatorial pursuit divers shape their

daily schedule around time of day and the contingencies of weather.

Conclusion.—Flightless Cormorants represent products of an evolutionary history that occurred within the context of strong geographical isolation and a unique set of climatic and oceanographic conditions. Behavior patterns are constrained by flightlessness, a unique factor among the 27 cormorant species. Colony occupancy and the occurrence of courtship behaviors were influenced primarily by time of day, whereas preen, wings spread, rest posture, and back sleep were most influenced by weather variables. Gular flutter, an indicator of thermal stress, increased with solar flux, time of day, and barometric pressure but decreased with wind speed. In contrast to the behavior of other marine birds, including other species of cormorants, the behavior of Flightless Cormorants is little influenced by tide.

Our study occupied only a short interval toward the beginning of the most active period of breeding during a La Niña year. Future investigations should examine the timing of behavior by Flightless Cormorants during other seasons, and during "normal" and El Niño years, especially in view of threats to the survival of this species in the face of global warming. In view of these threats, future work also should include time budget analyses for individual birds to determine how solar flux and other environmental factors influence the quantity of time spent thermoregulating at the expense of reproductive activity.

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ECOLOGY, BEHAVIOR, AND REPRODUCTION OF AN INTRODUCED POPULATION OF RED-VENTED BULBULS (*PYCNONOTUS CAFER*) IN HOUSTON, TEXAS

DANIEL M. BROOKS[1]

ABSTRACT.—Results are reported from a citizen-science program to study the ecology, behavior, and reproduction of an invasive population of Red-vented Bulbuls (*Pycnonotus cafer*) in Houston, Texas. The most frequent behaviors are foraging ($n = 69$), resting ($n = 45$), and calling ($n = 29$). The entire population occurred in urban areas. Bulbuls consumed berries ($n = 8$ species), fruits ($n = 5$), flowers ($n = 5$), and buds ($n = 4$); some insects are also included in the diet. Nine of the 20 species of identified plants consumed are exotics found within the native range of the bulbul, six are exotics found outside the native range, and five are native Texas species. The most common of the 35 species of plants that bulbuls perched in are bamboo (*Bambusa* sp.), crape myrtle (*Lagerstroemia indica*), edible fig (*Ficus carica*), and tallow (*Sapium sebiferum*). Flock size averaged 2.3 birds/flock (range = 1–22) and the largest flocks (12–22 birds) are in late summer and early winter. Bulbuls are not migrants; peak observations are during spring and summer, with lower numbers during October. General biology is similar between Houston bulbuls, native populations in Asia, and other invasive populations in the Northern Hemisphere. This alien population is not a serious agricultural pest or disperser of weedy seeds, does not compete with native species, and has not expanded beyond the Houston region in the continental United States. *Received 27 February 2013. Accepted 27 May 2013.*

Key words: avian ecology, citizen-science, invasive species, *Pycnonotus cafer*, Red-vented Bulbul.

The effects of invasive species upon native species and communities range from unharmful to devastating (Lockwood et al. 2007). The brown tree snake (*Boiga irregularis*), invasive to Guam among other Micronesian islands, is devastating to both endemic bird communities and human populations (Fritts and Rodda 1998). Monk Parakeets (*Myiopsitta monachus*), while not especially harmful to native birds, have caused extensive economic loss from their massive twig nests causing damage to electrical lines (Newman et al. 2008). Other invasive species such as European Starlings (*Sturnus vulgaris*) out-compete native cavity-nesting birds for limited nest sites (Cabe 1993).

The Red-vented Bulbul (*Pycnonotus cafer*; referred to as "bulbul" herein) is native to Pakistan, India, and Sri Lanka eastward to Viet Nam through southern China (Islam and Williams 2000, Fishpool and Tobias 2005). Throughout its native and introduced range, this species is found in a variety of habitats, including urban gardens and secondary growth (Islam and Williams 2000, Fishpool and Tobias 2005). Perhaps owing in part to its eurytopic habitat association, it is an established invasive species in areas of the Middle East and various tropical Pacific islands (Long 1981, Fishpool and Tobias 2005). A previously unstudied population is established in Houston, Texas.

In parts of their introduced ranges, bulbuls feed on a variety of cultivated plants and thus are in direct conflict with humans (Islam and Williams 2000). Additionally, invasive bulbuls are potential dispersers of weedy seeds and may compete with native birds (Islam and Williams 2000). While invasive populations of bulbuls have been studied in Polynesia (Dhondt 1976a, b, 1977; Watling 1977; Pernetta and Watling 1978) and Oahu (Bremer 1977; Williams 1983, 1987; Williams and Giddings 1984), ecological studies of invasive populations on any continental land mass are lacking.

Relatively little work has been done with alien birds in the state of Texas (c.f., Brooks 2009, 2012). In June 2008, I initiated the Texas Invasive Bird Project, a citizen-science study targeting six avian species invading the state, one of which is the Red-vented Bulbul. Using reports generated from this project, the objective of this study is to elucidate the ecology, behavior, and reproduction of the Red-vented Bulbul in Houston, Texas, USA, while hypothesizing this species is not currently an ecological threat in Houston.

METHODS

To document invasive bird species in the area, I designed a questionnaire to be made available at several local birdwatching clubs, annual birdwatching festivals, circulated on Texas birdwatching

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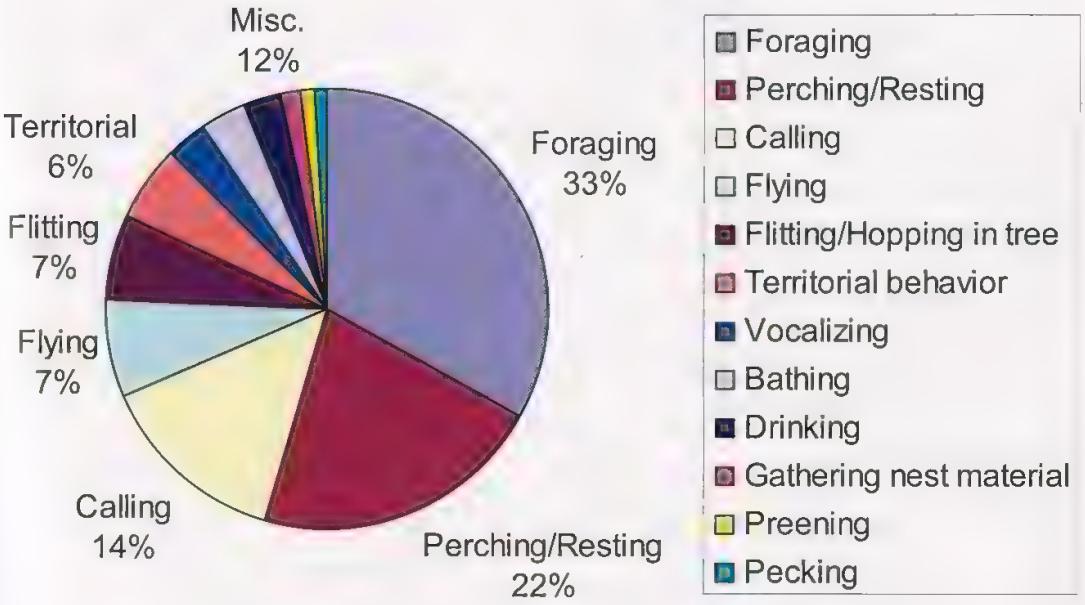

FIG. 1. Bulbul activity patterns in Houston, Texas (Jun 2008–May 2012).

internet list-servs, and posted on-line at: www.hmns.org/files/invasivebirds.doc. The majority of the questionnaire respondents fell into two broad categories: (1) birdwatchers who are familiar with bulbuls, and (2) horticulturists who maintain diverse gardens and enjoy the urban wildlife that visits. In cases of wildlife that could not be identified, most of the respondents sought help on the internet which ultimately led to the bulbul photograph on the questionnaire. When returning the questionnaire, most respondents indicated they were enthusiastic about being able to identify the bird they saw.

Respondents seemed honest and conservative; if they did not know the answer to a given question they left it blank or stated they did not know. In most cases, respondents included voucher photographs and/or a written description of the birds and habitat to confirm documentation. I proofed the citizen scientist data for accuracy to ensure that birds, plants, habitat, and abiotic parameters were accurately designated and identified by: (1) examining all photographs and (2) ground truthing ~15% of the sites via direct visits. In some cases, I was able to obtain plant, habitat, and abiotic parameter data from submitted photographs if those portions of the questionnaire were left blank. In a few cases where plants were not obvious, I confirmed species designation with museum staff botanist (N. Greig).

I tabularized results in respective sections of a database for analyses. Occasionally responses were anthropomorphized, whereupon I interpreted the information accordingly (e.g., ''two birds in love who spent the day chatting away'' = ''a vocalizing pair''). In cases where reports provided numerical data in feet, I converted the data to meters. In cases where numerical data were provided as a range, I used the average between the minimum and maximum (e.g., perched 20–25 feet = 22.5 feet = 6.8 m). I did not include insufficiently completed questionnaires in analyses.

Data used herein span 4 years (Jun 2008–May 2012) but information is still being collected for possible future analyses. Data for the distribution portion of this study spanned through February 2013 to ensure more thorough documentation of dispersal. I obtained older dates preceding the initiation of the study (Jun 2008) from respondents and eBird reports (eBird 2013).

RESULTS

The most frequent three of the 12 activities (Fig. 1) are foraging (n = 69), perching or resting (n = 45), and calling (n = 29).

Foraging.—Bulbuls consume berries (n = 8 species), fruits (n = 5), flowers (n = 5), and buds (n = 4; Table 1). Nine (45%) of the 20 species of identified plants are exotics found within the native range of the bulbul, whereas six (30%) are

TABLE 1. Plant species consumed and perched on by invasive Red-vented Bulbuls (*Pycnonotus cafer*) in Houston, Texas (2008–2012).

Plant species	Latin name	Origin[b]	Plants consumed[a]				Plants perched on			
							Numeric data	Relative data		
			Berry	Fruit	Flower	Bud	Perch ht (m)[c]	Low	High	No data
American beautyberry	*Callicarpa americana*	N	3							1
American elm	*Ulmus americana*	N							1	
American sycamore	*Platanus occidentalis*	N							1	
Azalea	*Rhododendron* sp.	N					1.3			
Bald cypress	*Taxodium distichum*	N						1	1	
Bamboo	*Bambusa* sp.	EB					5.2 (2.5–10) 8			6
Bamboo, Sacred	*Nandina domestica*	EB	1							1
Bauhinia	*Bauhinia* sp.	EB			6		2.5			7
Camphortree	*Cinnamomum camphora*	EB		1						2
Common hackberry	*Celtis occidentalis*	EB					8			1
Crapemyrtle	*Lagerstroemia indica*	EB			4	3	3.8 (1.7–6.7) 5		1	8
Edible fig	*Ficus carica*	EB		10			1.5		1	10
Elderberry	*Sambucus nigra*	N					3.2			
Firethorn	*Pyracantha* sp	EB	1							
Hibiscus, Chinese	*Hibiscus rosa*	EB			1		2.1 (1.5–2.7) 2			
Hibiscus, Terri's pink mallow	*Hibiscus paramutabilis*	EB				1	1.5			
Jasmine, Orange	*Murraya paniculata*	EB					1.8			
Kumquat	*Fortunella* sp.	EB					1			
Lantana	*Lantana camara*	EO	3							1
Lilac Chastetree	*Vitex agnus castus*	EO					1.8			
Magnolia, (Japanese)	*Magnolia* sp.	EB				2	3.6 (2.7–4.5) 2			1
Mallow, Wax	*Malvaviscus drummondii*	N	1							1
Mimosa	*Albizia* sp.	EB						1	1	
Mulberry	*Morus alba*	EB					2.4			
Oak	*Quercus* sp.	N					12.9 (6–28) 4		2	
Palm, Washington fan	*Washingtonia robusta*	EO		1	1					
Palm, Parlor	*Chamaedorea elegans*	EO		1			1.3			
Passion flower vine	*Passiflora incarnata*	N								1
Pear	*Pyrus* sp.	EO				1	7.6			1
Pecan	*Carya illinoinensis*	N					9.4 (5–12.5) 3		3	2
Pine	*Pinus* sp.	N						1		
Pine, Loblolly	*Pinus taeda*	N								1
Plum, Mexican	*Prunus mexicana*	N							1	
Redbud	*Cercis canadensis*	N					2.4			

TABLE 1. Continued.

Plant species	Latin name	Origin[b]	Plants consumed[a]				Plants perched on			
							Numeric data	Relative data		
			Berry	Fruit	Flower	Bud	Perch ht (m)[c]	Low	High	No data
Redcardinal	*Erythrina herbacea*	N			1		2.7			
Snailseed	*Cocculus carolinus*	N	1							
Tallow, Chinese	*Sapium sebiferum*	EB					20.2 (9–35) 6	2	2	2
Tomato	*Solanum lycopersicon*	EO	1							
Trumpet Creeper	*Campsis radicans*	N					3			
Yaupon	*Ilex vomitoria*	N	1							
Yucca, False	*Hesperaloe parviflora*	EO	1							1
Unidentified tree/shrub			1	1			3.4 (0.5–6.1) 7	1	2	5

[a] The number of reports (e.g., 1 or 2) for each food type is quantified in respective columns.
[b] EB = Exotic plant whose native range lies within the native distribution of the bulbul; EO = Exotic plant whose native range lies outside the native distribution of the bulbul; N = Native Texas plant.
[c] In cases where plant/perch height sample size was >1, data are reported as: mean (range) sample size.

exotics found outside the native range and five (25%) are native Texas plants (Table 1).

There are 12 cases of insectivory, at least six of which involve gleaning insects from a plant, including bamboo (*Bambusa* sp.) twice, and once each for edible fig (*Ficus carica*), Rangoon creeper (*Quisqualis indica*), and tomato (*Solanum lycopersicon*). Insects found on tomatoes were identified as stink bugs (Pentatomidae or Coreidae). Other modes of foraging include sallying for flying insects ($n = 2$) and masticating insect prey on the ground ($n = 1$) or a utility line ($n = 1$).

Habitat and Perch Use.—Nearly all ($n = 74$, 96%) of the 77 reports describe residential suburb as the primary habitat. Other cases include small fragments of secondary growth within a mosaic of urban parkland along White Oak Bayou ($n = 2$) and an individual flying across the street between parkland habitat and suburbs ($n = 1$).

Bulbuls perch on 35 species of plants. Species most frequently used for perching are bamboo and crape myrtle ($n = 14$ each), edible fig and tallow ($n = 12$ each, Table 1). Bulbuls perch in 15 different plant species (43%) native to Texas, 15 species (42%) of exotics found within the native range of the bulbul, and 5 species (14%) of exotic plants found outside the native range (Table 1). Mean perch height on plants is 6.2 m (range = 1.7–14.5, $n = 19$; Table 1). Of the 10 different categories of abiotic perches, the most frequent are phone and utility wires ($n = 17$) followed by bird baths and water fountains ($n = 9$; Table 2). Mean perch height on abiotic structures is 3.4 m (range = 1.2–9.1, $n = 23$; Table 2).

Seasonal Flock Dynamics.—Bulbuls are nonmigratory residents that are present throughout the year (Figs. 2, 3). The largest flocks (12–22 birds; Fig. 2) occur August–September and December–January. The flock of 22 birds in August was attracted by the fruits of a Washington fan palm (*Washingtonia robusta*). When the palm was removed the following day, the flock left the area.

Flock size averages 2.3 birds/flock (mode = 2, range = 1–22). There are no significant differences between pairs and singletons on any given month except for March ($X^2 = 3.6$, df. = 1, $P = 0.05$; Fig. 3). However pairs of birds are more frequent than singletons each month except for late summer through fall (Aug, Oct, and Nov) when singletons are more frequent (Fig. 3). Pairs of birds ($n = 63$) are significantly more frequent than singletons ($n = 40$; $X^2 = 5.3$, df. = 1, $P = 0.02$) when considering totals.

TABLE 2. Abiotic structures used for perching by invasive Red-vented Bulbuls (*Pycnonotus cafer*) in Houston, Texas (Jun 2008–May 2012).

Abiotic structure	Numerical data	Relative data	
	Perch height (m)[a]	Low	High
Bird feeder		3	
Water fountain/bath	3 (3) 9		
Vegetable garden		1	
Tomato garden cage	1.2		
Fence (chain link, decorative, trellis)	1.5 (0.5–2.3) 7		
Metal stake	2		
Phone/light pole			3
Utility/phone wire	7.2 (6–9.1) 4		13
Roof edge			1
Aluminum window frame	6.8		

[a] In cases where structure/perch height sample size was >1, data are reported as: mean (range) sample size.

Reproduction.—Courtship display was observed 18–25 March. Observers documented the gathering of nest material (e.g., pulling twigs from gutters) on 23 and 26 March, 12 April, and 17 May. On the latter date, the pair of bulbuls harassed a Blue Jay (*Cyanocitta cristata*) that was too close to the nest site. Single nests in early May and mid-July were in crape myrtle 3.3 and 3.0 m off the ground, respectively. The first was constructed of tightly woven grasses and pliable vegetation and the second was in the center of the tree. The pair observed in July repeatedly chased a Great-tailed Grackle (*Quiscalus mexicanus*) that would not leave the area, and they also mobbed an unidentified hawk flying over.

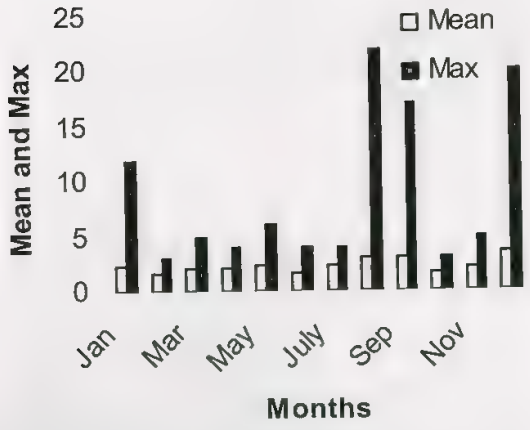

FIG. 2. Monthly mean and maximum values for flock size of bulbuls in Houston, Texas (Jun 2008–May 2012).

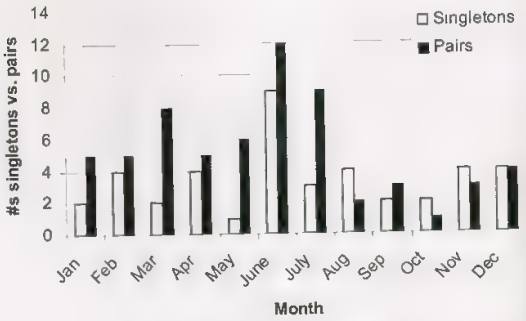

FIG. 3. Monthly abundance of singletons vs. pairs of bulbuls in Houston, Texas (Jun 2008–May 2012).

Observers reported observations of fledglings as follows: a female with fledgling (Mar), two adults with smaller sub-adult (21 Apr), a fledgling admitted to a wildlife rehabilitation clinic (24 Apr), two fledglings being fed crape myrtle (four observations spanning 13–17 Jul), a female observed feeding a ~7.5 cm tall fledgling (21 Jul), a fledgling admitted to a wildlife rehabilitation clinic (18 Aug), and a young bird that appeared to be begging for food (1 Sep).

Distribution.—A total of 117 different sites where bulbuls have been observed were plotted on a map (Fig. 4). Yet, the origin of the bulbuls in Houston is unknown. Ostensibly, some could have arrived on large cargo barges from southern Asia that docked in the Houston Ship Channel along the eastern reaches of Buffalo Bayou (Fig. 4). The bulbuls would then have gradually dispersed west and north along the bayou system towards White Oak Bayou, where the birds found plenty of safe urban gardens in an area known as the Heights (essentially north of White Oak Bayou and west of Little White Oak Bayou).

DISCUSSION

Comparisons with Bulbuls in their Native Range.—Only five of the 20 identified plants which bulbuls fed on are native to Texas. Nine of the remaining 16 are exotics found within the bulbul's native range. Fishpool and Tobias (2005) identified 65 plant genera known to be consumed by bulbuls, although feeding on exotic plants was not distinguished from those taken within the native range. Methods of insect capture and handling (i.e., sallying, gleaned from a plant, or brought to the ground for mastication) are also among the foraging behaviors observed in natural

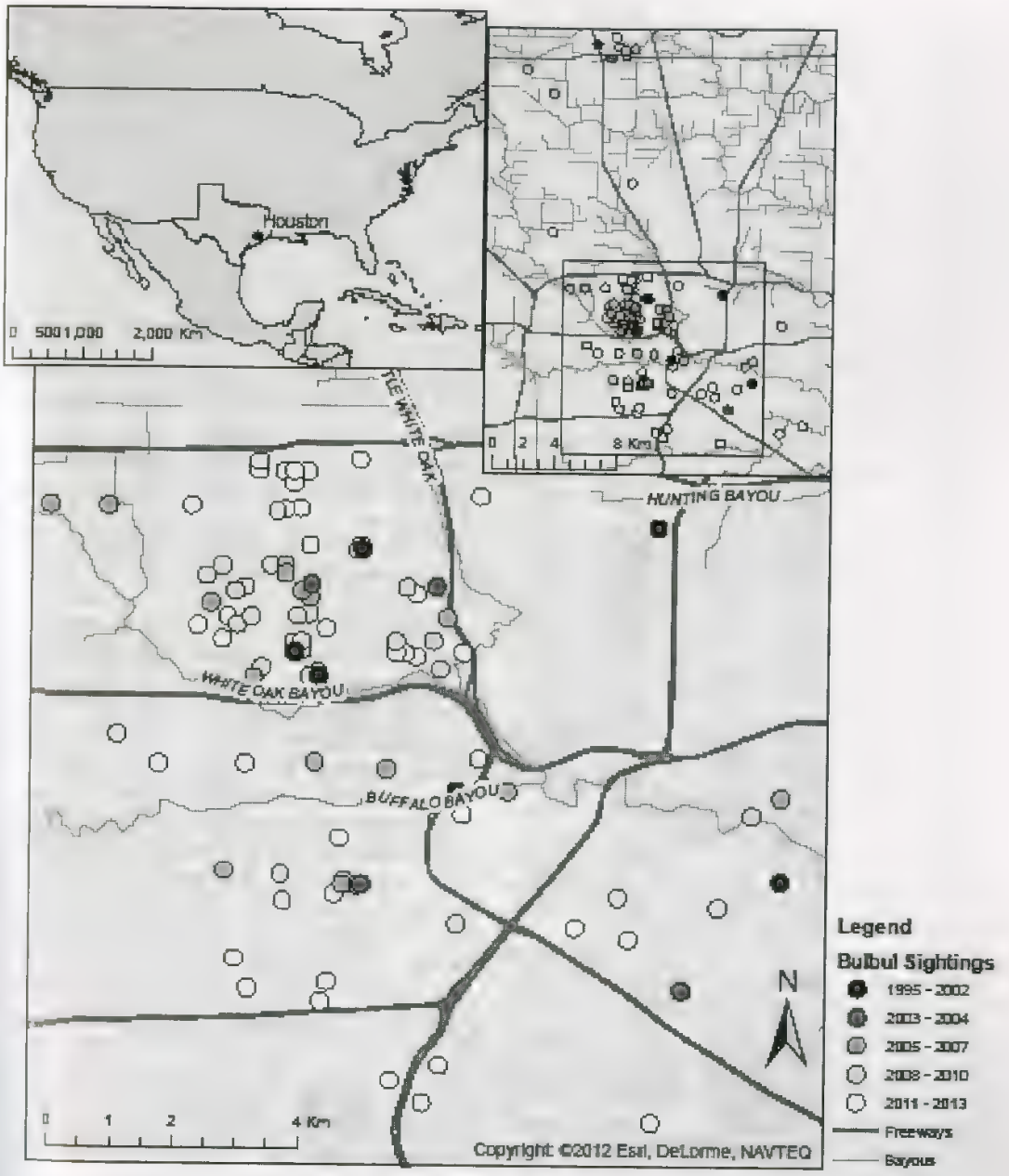

FIG. 4. Distribution of bulbuls within the city of Houston, Texas (Jun 2008–Feb 2013).

populations (c.f., Islam and Williams 2000, Fishpool and Tobias 2005).

In their native range, bulbuls are found from 0 to >2,000 m from forest edge, as well as gardens and cultivated areas (c.f., Islam and Williams 2000). Virtually all of the bulbuls in Houston are found in residential gardens at sea level, with the only other cases being fragments of secondary habitat in edge situations. Bulbuls in this study use a diverse array of plants (35 species) as perches. Although bulbuls perch in 15 species of native Texas plants and 15 indigenous to their native range, the four most commonly used as perches are invasive species (bamboo, crape myrtle, fig, and tallow) found within the natural range of the bulbul. These results corroborate the

model of invasive species succeeding in human-altered environments where ecological niches are available that were unexploited by native species (c.f., Lockwood et al. 2007).

In India and Pakistan, bulbuls form pairs from February through November (Ali and Ripley 1971). Similarly, in this study, pairs of birds are more abundant than singletons from January–September. In their native range, bulbuls are not highly gregarious during breeding season and are usually seen in pairs or small family parties, with larger gatherings (20–100 birds) occurring when food is seasonally abundant during the non-breeding season (c.f., Islam and Williams 2000). In Houston, the largest flocks are much smaller (maximum = 22) but are similarly observed outside the breeding season.

Bulbuls are year-round residents in Houston, as well as in their native range (Ali 1977). However, seasonal movements in their native range occur in response to environmental conditions, including following rain and moving altitudinally in response to seasonal shifts in temperature (Fishpool and Tobias 2005). It is possible that some seasonal local movements occur in the Houston populations, as some of the reports indicated that bulbuls are usually present during the same period interannually. For example, we observed a pair of birds on our property 18–22 March 2007 and again one year later on 24 March 2008. Whether this was the same pair of birds is unknown, yet such observations warrant banding studies to learn more about seasonal site fidelity.

Comparisons with other Invasive Populations of Bulbuls.—Red-vented Bulbuls are known to thrive in Arabia (U.A.E., Kuwait, Qatar, and Oman), Polynesia (Fiji, Samoa, and Tonga) and Oahu, Hawaii, with failed attempts to colonize parts of Australia and New Zealand (Long 1981, Fishpool and Tobias 2005). The congeneric Red-whiskered Bulbul (*P. jocosus*) is also an established invasive in parts of the Nicobar and Mascarene island chains, Australia, Singapore, Oahu, southern California, and Florida (Islam and Williams 2000). Overall, the Houston population is similar to other invasive populations of both Red-vented and Red-whiskered bulbuls. While subtle differences in breeding season occur between invasive populations of the two species, more extreme differences are found between Northern versus Southern Hemisphere populations regardless of species.

The Red-vented Bulbuls in Houston share foraging and roosting techniques with other invasive populations of bulbuls (Bremer 1977, Islam and Williams 2000); they exhibit similar general foraging habits (Carleton and Owre 1975, Watling 1977, Islam and Williams 2000) and inhabit similar suburban habitat, although Red-whiskered Bulbuls also utilize citrus orchards (Watling 1977, Williams and Giddings 1984, Islam and Williams 2000).

While dates of pair formation are similar between Red-vented Bulbuls in Houston and in their native range, invasive populations in the Southern Hemisphere form pair bonds November–January (Dhondt 1977, Watling 1977). A similar pattern is evident for Red-whiskered Bulbuls, with Northern Hemisphere pairs bonding winter through summer (late Feb–Jul in Florida, Jan–Aug in Oahu), and August–March in Australia in the Southern Hemisphere (Berger 1975, Carleton and Owre 1975, Long 1981, Islam and Williams 2000).

Red-whiskered Bulbuls begin nest-building in February in Oahu and Florida, and Red-vented Bulbuls begin in March in Oahu, Fiji (Carleton and Owre 1975, Watling 1977, Islam and Williams 2000), and Houston. Red-vented Bulbul fledgling periods are similar between Houston (Mar–Sep) and Oahu (typical months: Apr–Jun, extreme: Jan–Oct; Islam and Williams 2000). The fledgling period for Red-whiskered Bulbuls in Oahu is typically March through May (extreme: Feb–Aug), although late fledglings are rare in Oahu, and apparently do not occur at all in Florida (Islam and Williams 2000).

Both species are non-migratory (Long 1981). Flocks of 20–100 will gather at resource blooms (Watling 1977, Islam and Williams 2000), reflecting the case in Houston when a flock of 22 Red-vented Bulbuls gathered to feed at a fruiting Washington fan palm but left when the palm was removed.

Are Introduced Bulbuls a Threat in Houston?—Bulbuls are a well-established invasive species considered agricultural pests in parts of their invasive range such as Oahu. This reputation is because of their habit of consuming orchid and hibiscus buds (Denny 2010), two plants commercially farmed in Oahu. For example, bulbuls and the invasive Japanese White-eyes (*Zosterops japonicus*) damaged up to 75% of dendrobium orchids in plantations (Hawai'i Audubon Society 1989, Cummings et al. 1994). However, neither

orchids nor hibiscus are commercially farmed in Houston, thus bulbuls are not an economic threat to a Houston-based exotic plant industry.

Bulbuls are potential dispersers of noxious weedy seeds (Islam and Williams 2000). For example, captive bulbuls of the invasive population in Fiji successfully germinated the following species: spiked pepper (*Piper adancum*, 90% germinated), guava (*Psidium* sp., 87%), cape gooseberry (*Physalis peruviana*, 35%), and prickly nightshade (*Solanum torvum*, 28%; Watling 1977). While tropical weedy species are poorly established in Houston, it is important to note the potential that bulbuls have as successful seed dispersers. Additionally, tallow (a strongly *r*-selected invasive tree), despite being one of the most frequently used perch types, is not consumed by bulbuls, thus not likely to be dispersed.

Although Watling (1977) did not consider invasive bulbuls in Fiji to be a threat to native birds, Islam and Williams (2000) indicate they may be potentially harmful competitors in other areas. For example, certain lowland dwelling populations of O'ahu 'Amakihi (*Chlorodrepanis flava*; Lindsey et al. 1998) and Hawai'i 'Elepaio (*Chasiempis sandwichensis*; VanderWerf 1998) may both compete with introduced bulbuls in Oahu. Reports involving interspecific interactions in the population in Houston were very limited and therefore not described in detail. Of note however, aggression is displayed towards smaller more passive species at bird feeders, and larger species too close to a nesting pair which can stimulate mobbing behavior. Overall, Houston's population of bulbuls shows little agonistic aggression towards other species of birds.

Approximately one-half of all locations of bulbuls are concentrated in the Heights (north of White Oak Bayou and west of Little White Oak Bayou; Fig. 4). Several recent sightings (since 2011) are south of Buffalo Bayou, suggesting the range is expanding to the south. A second population in the Greenspoint area of Houston (far north, right inset; Fig. 4), although smaller than the Heights population, has also been present since the mid-1990s (eBird data, 7 Feb 2013). The origin of the population in Greenspoint is unknown, but it is possible that some escaped from captivity. There are two locations where bulbuls were documented midway between the Heights and Greenspoint populations, suggesting these two populations may be contiguous in the future.

It appears that Houston's introduced bulbul population is not currently an environmental threat, although they should be closely monitored in light of issues with other invasive populations. In the continental United States, this invasive species has not expanded beyond the city of Houston, and the most concentrated part of the population is stably harbored within a relatively small area (<20 km^2; Fig. 4). Maximum flock size is smaller, and large flocks are not encountered with any frequency in Houston, when compared to native Asian populations. Additionally, Houston's bulbuls do not deplete populations of native plants for consumption. It is possible that the birds are selecting species from within their natural range in Asia to perch in (bamboo, crape myrtle, fig and tallow) or consume (nine of 20 species).

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Short Communications

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Rapid sampling of Males and Territories by Female Northern Lapwing, *Vanellus vanellus*

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ABSTRACT.—In many birds, females prospecting for high quality breeding resources have to inspect a number of males and their territories to make a good mating choice, yet in the face of competition with other females, the search time should be minimized. The sequential sampling of potential mates and territories by females is seldom witnessed. In a study of breeding Northern Lapwings, *Vanellus vanellus*, in Norway, we observed a female during the pair-formation period visiting seven territories in 105 mins, spending 15–20 mins on each of six territories pecking food from the ground and watching the resident male performing nest-scraping displays. One of the males was already mated, and on this territory the prospecting female spent only ~2 mins. The observations show that female Northern Lapwings are potentially able to sample a high number of available territories in only a few hours. *Received 7 May 2013. Accepted 29 July 2013.*

Key words: breeding behavior, mate prospecting, Northern Lapwing, Norway.

Mate choice can be represented by optimal models, in which fitness gains from choice of high quality mates and the resources they offer are balanced by costs of searching for mates (Parker 1983, Real 1990, Gibson and Langen 1996, Castellano and Cermelli 2011). Under strong time constraints, such as in a highly seasonal environment, there is a trade-off between the number of potential mates that can be sampled and the urgency for making a decision before an attractive and resourceful mate is occupied by another (Slagsvold and Lifjeld 1997, Castellano and Cermelli 2011). Two main strategies for mate choice have been discussed; either the mate prospector compares the available possible mates within a given area and returns to choose the best one or, makes a decision once an encounter is made with a potential mate that exceeds an acceptance threshold held by the searcher (e.g., Janetos 1980, Parker 1983). In the face of high search costs (e.g., high competition for mates), the latter strategy may be the most rewarding (Real 1990). Some studies of birds have suggested that time and energy costs of search may restrict mate sampling opportunities for females to the extent that they are forced to choose sub-optimal or maladaptive mating options (Slagsvold et al. 1988, Dale et al. 1992, Slagsvold and Dale 1994).

From studies in southwestern Norway, we have found that in Northern Lapwing, *Vanellus vanellus* (hereafter lapwing), males defend all-purpose breeding territories, and the earliest females become resident on territories within a few days after territories have been established by the males (Byrkjedal et al. 1997, Grønstøl 2003). In 1998 and 1999 exact time of settlings were recorded in our study area, and in these 2 years it took a territory-holding male on average 3.2 days (±3.49 SD; 17 territories) and 1.4 days (±2.70 SD; 22 territories), respectively, to obtain a female. This indicates the shortness of the time window available for female mate choice, although a number of females ended up as secondary females to already mated males. Color-banded females in our studies have been observed to visit 2–4 territories before settling, but the rate of mate-sampling by these females has not been possible to record. On 24 March 2000, while mapping male territories from a vantage point in part of a study area at Jutland, Jæren, (see Grønstøl 2003 for details on site and study), we observed a female lapwing visit seven territories in a time span of 105 mins. This observation, described below and in Figure 1, indicates that female lapwings may sample many males and territories in an astonishingly short time.

The female was easily recognizable from an unusually large white patch on each wingtip (Fig. 1). She appeared on the first territory at 0930 CET (Central European Time). The male on this territory was already mated, but egg-laying had not yet started. The male went into a nest-scraping display (see Shrubb 2007 for a description of this type of display) near the new female, which stood watching. The resident female

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FIG. 1. Seven territories visited by a female Northern Lapwing on 24 March, 2000, Jæren, in the time span from 0930–1115 CET (Central European Time). The female was recognizable from white wing tips (inserted sketch). Arrows and numerals indicate the sequence with which the female visited the territories. Individuals resident on the territories during the female visits: M = one male, M + F = one male, already mated to one female. Stone fences and dirt roads are indicated.

assumed an upright posture apparently signalling aggression towards the newcomer, and the latter left the territory after only a couple of minutes. Flying across two territories, it landed in another territory on which there was only a male present. The male immediately went into scraping display. The female walked slowly about, watching the male while at the same time pecking for prey, including a couple of earthworms (Lumbricidae) which she ate. The female spent about 15 mins on this territory before flying over to a next, also this territory with only a single male present. Here, the same behavior was repeated by both birds: the male making scraping displays while the female partly fed, partly watched the male. Again after about 15 mins, the female left for another territory, and this repeated itself until she had visited seven territories. The same behaviors were seen in each case, and each visit lasted 15–20 mins. Finally, the female left the study area and was not later observed. Whether she finally bred in the general area we are unable to tell, but there were many lapwing territories in the adjacent fields beyond our study area.

The observation was made at a time of the season when most of the males had established territories but not yet acquired a mate, and indicates that females may sample potential mates and perform "test-feeding" on male territories in the course of a short time span. We do not know whether lapwings compare as many males and territories as possible before a choice is made, or if they mate after having found a male and the resources held by him to exceed a certain threshold. However, with a sampling rate of four territories per hour, a female could potentially visit and acquaint herself with many tens of territories in a day or two. Lapwings often breed in aggregations of 15–20 contiguous territories (Cramp and Simmons 1983, Byrkjedal et al. 1997), which was also the case on the present study area. The rapid mate-sampling we observed indicates that a female lapwing could sample all territories in an aggregation within only a few hours. The observed female wasted no time crisscrossing the field but rather made her visits apparently meticulously by sampling territories that were more or less contiguous to one another.

In the present study area, nesting as well as chick-rearing and most of the feeding by the pair took place within the territories, and choosing a mate with a high quality territory must clearly be of importance to the female lapwings. To our knowledge, ours is the first reported mate-sampling rate in a non-lekking shorebird. The rapid sampling rate we observed is similar to what was found in female European Pied Flycatchers, *Ficedula hypoleuca*, in which up to seven potential mates could be sampled in an hour (Dale et al. 1992), and the potential number of mates that could be visited by the female lapwing observed by us may exceed that found in other bird studies, including lekking species (Jennions and Petrie 1997).

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Geographical Differences in Nesting Habitats of Terek Sandpiper (*Xenus cinereus*)

Włodzimierz Meissner,[1,4] Mikhail Golovatin,[2] and Sergey Paskhalny[3]

ABSTRACT.—Data concerning 303 nests of the Terek Sandpiper (*Xenus cinereus*) from 58 breeding sites in different parts of Russia and Ukraine were analyzed. Among them 196 were found in the western and 107 in the eastern part of this species' breeding range. In the eastern part, 61% of nests were placed in forests or within bushes, while in the western part only 8% of them had such location. Moreover, in the eastern part the species seems to avoid natural open habitats in spite of their availability, whereas in the western part of the breeding area nests were built mostly in open habitats, like meadows, pastures, or sandbanks dominated by sparse and low vegetation. Therefore, western and eastern populations of the Terek Sandpiper differ in nesting habitat selection. This is an exception among related species of the family Scolopacidae, for which different nesting habitats were reported only occasionally. *Received 19 November 2012. Accepted 4 May 2013.*

Key words: ecological plasticity, Eurasia, habitats, nest, *Scolopacidae*.

Breeding area of the Terek Sandpiper (*Xenus cinereus*) covers a vast territory from the Baltic Sea coasts to the Chukotka Peninsula (Golovatin et al. 2010). The population is roughly estimated at between 0.1 and 1 million individuals (Kirby and Delany 2009), but information on this species is very limited. In the Web of Knowledge database (Science Citation Index Expanded) in section "topic" there are no records concerning breeding biology or nesting habitat of this species (Web of Knowledge 2012). Despite the fact that the Terek Sandpiper breeds across large part of northern Eurasia, its nesting biology remains poorly described (Meissner et al. 2012). And although data on this species could be found in different reports on local avian fauna, there is a lack of any analysis about any aspects of nesting period, except the recent summary of data found in Russian literature (Meissner et al. 2012).

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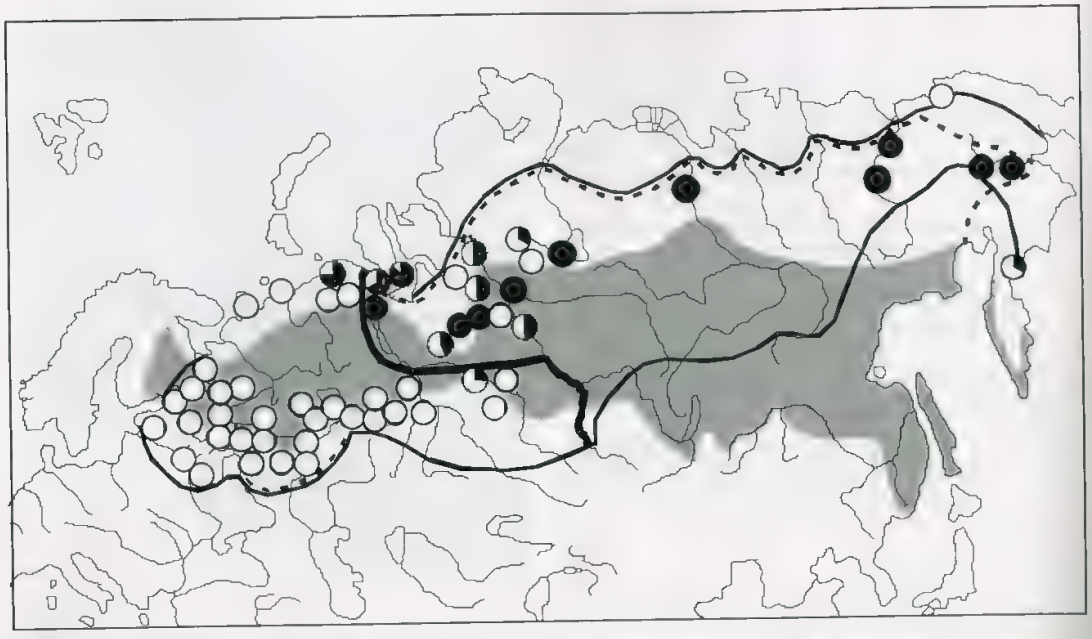

FIG. 1. Distribution of Terek Sandpipers' nest sites analyzed in this study. White and black parts of the pie-charts specify sites with nests found in open habitats and in woodlands, respectively. Gray shows the area of continuous forest zone, where mean forest cover exceeds 50% (according to Lavrenko 1947, Milkov 1977). The dashed line outlines the region where forests are distributed along river valleys (forest cover in this landscape is below 50% but in floodplain is more than 50%; Lavrenko 1947). Thin solid line shows breeding rage of this species according to Golovatin et al. (2010). Division line between the western and eastern parts of the breeding range is shown as a thick solid line.

The Terek Sandpiper breeds in lowland valleys of northern boreal forests and forest tundra, mainly along rivers on floodplains with flooded meadows and marshes with patches of scrub, avoiding mountains, fast rocky streams, extensive open spaces and tall dense forest (Cramp and Simmons 1983). Strong preference of Terek Sandpipers to river banks or shores of different water bodies was known from all parts of their breeding range (e.g., Grote 1938, Kozlova 1961, Morozov 1998). Preliminary analysis of published data on breeding habitats of this species suggested substantial differences between the birds from the eastern and western parts of the breeding range. In Belarus and in the western part of Russia, the Terek Sandpiper prefers overgrazed floodplain pastures and meadows with sparse vegetation for breeding (Mischenko and Sukhanova 1998, Nikiforov 1998). It also often nests on bare ground at sites with complete absence of vegetation (Zubakin et al. 1998). Farther to the east, this species breeds not only on sandy river banks, but also in oak or alder woods growing along rivers (Ivanchev and Kotyukov 1999), while in the Yenisei basin and farther to the east, it prefers waterlogged woodlands on the river banks and around lakes (Grote 1938, Labutin et al. 1988, Rogatcheva et al. 1988, Volkov 1988).

In this paper we summarize information on the nesting habitat of the Terek Sandpiper based on our own data and descriptions of nests published in Russian literature. Special emphasis was put on verification of the presumption of differences in habitat choice between the eastern and western part of the species' breeding range.

METHODS

For this study, the breeding range of the Terek Sandpiper was divided into western and eastern regions. The border runs along the Ural Mountains and farther south along the boundary between the middle and southern taiga subzones (Lavrenko 1947) and to the east as far as the Yenisei River (Fig. 1). The southern part of this division, which runs southeastwardly from the Ural and ends at about 85 °E is different than described in an earlier publication (Meissner et al. 2012), where it ran farther along 60 °E south from the Ural. The new division takes into account taiga subzones instead of an arbitrary line running as a continuation of a line depicted by the Ural

TABLE 1. Classification of nesting habitats of the Terek Sandpiper according to Meissner et al. (2012).

Symbol	Description	Habitat type
Fore	different types of forests, mainly with domination of arborescent willow *Salix* sp., aspen *Populus* sp., larch *Larix* sp., alder *Alnus* sp. and chosenia *Chosenia* sp.	Woodland sites with nests placed in forest or bushes
Bush	willows or dwarf birch bushes	
Coas	sandy or pebbly banks, coasts or spits with bare ground of sparse vegetation, often with drifted rubbish and remains of plants washed ashore	
Agri	agricultural areas (e.g., arable fields, peat fields, potato fields, open peat pits)	Open habitats with nests placed within vegetation, mainly low and sparse grasslands
Past	overgrazed pastures, wet meadows and sedges	
Anth	anthropogenic habitat including constructions (dams, embankments), exposed bottoms and shores of industrial ponds and lawns in human settlements	

Mountain range. The main difference in habitat between both types of taiga is development of undergrowth, which is sparse in the middle taiga and is well developed in the southern taiga (Milkov 1977, Ilina et al. 1985). This difference affects the structure of breeding bird communities and their density (Ravkin and Ravkin 2005) and may also influence nesting habitat and nest placement of the Terek Sandpiper (Meissner et al. 2012).

In this study, data on 303 nests from 58 nesting sites located in different parts of Russia and Ukraine were analyzed. Among them, 196 nests were found in the western and 107 nests in the eastern part of the breeding range. Descriptions of 41 nests were taken by the authors in the region of the lower Ob river basin. The rest of the data were obtained from published sources that described details of the nesting habitat (see appendix in Meissner et al. 2012). The number of nests found within each site varied from 1 to 33. Each nest was classified as occupying one of six types of nesting habitats, which were grouped into two main types: woodlands and open habitats (Table 1). Within 10 sites the Terek Sandpipers' nests were situated in both habitat types, whereas in others only in one of them (Fig. 1). Statistical analysis was performed according to Zar (1996), using STATISTICA 9.1 (StatSoft Inc. 2010).

RESULTS

The proportion of nests found in two main habitat types differs significantly between the separate parts of the breeding range (G-test, $G = 100.5$, $P < 0.001$). In the eastern part, 61% of nests were placed in forests or within bushes, while in the western part only 8% of nests were placed in these areas (Fig. 2). Outside the continuous forest zone, nests found in the large river valleys (Khatanga, Lena, Kolyma, Anadyr) were localized within woodlands (Fig. 1). In the western part of the breeding area nests were built in open habitats, like meadows, pastures, or sandbanks with sparse and low vegetation dominated (Fig. 2).

DISCUSSION

Differences in nesting habitat between the eastern and the western part of the breeding range of Terek Sandpipers might be attributed to the differences in the habitat structure between these two areas. This species occurs in the highest density in the large river valleys (Kozlova 1961, Golovatin et al. 2010), and river floodplains are

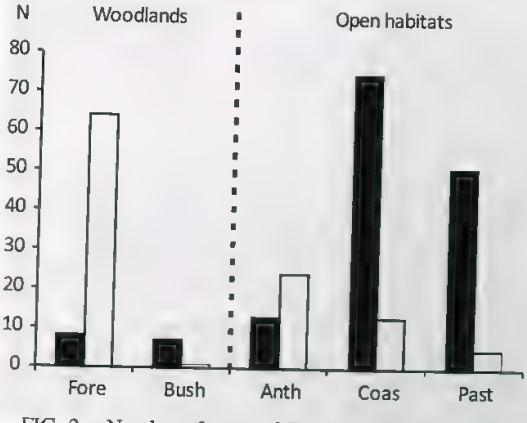

FIG. 2. Number of nests of Terek Sandpipers found in different habitats in the western (black bars) and the eastern (white bars) part of the breeding range. Abbreviations of habitat names are given in Table 1.

among the first habitats to be altered by expanding human populations (Nilsson and Dynesius 1994). Floodplains originally supported alluvial forests, but changes in land use have resulted in their rapid decline and development of an agricultural landscape (Abernethy and Turner 1987, Pott 1992). In the western part of the Terek Sandpipers' breeding range, within large rivers' floodplains, forest area is limited and open habitats dominate, with the exception of the Vyatka and middle Volga valleys (Milkov 1977). In these two regions, riverside forests remain and still cover an extensive area of the floodplains. In contrast to the Lower Ob, Terek Sandpipers' nests were not found in woodlands, but exclusively in open habitats (Sotnikov 2002, Zavyalov et al. 2007). In the eastern part of the breeding range, this species appears to avoid natural open habitats in spite of their availability (see Fig. 1). Therefore, it seems that western and eastern populations of the Terek Sandpiper differ in nesting habitat selection. This is an exception among related species of the family Scolopacidae, for which different nesting habitats were reported occasionally only in case of the Spotted Redshank (*Tringa erythropus*), Greenshank (*Tringa nebularia*), and Wood Sandpiper (*Tringa glareola*) (Hayman et al. 1987). These three species placed nests mainly in lightly-wooded forests, but rarely in more open habitats, like treeless uplands and blanket bogs (Hayman et al. 1987).

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Notes on the Incubation, Brooding, and Provisioning Behavior of Chuck-will's-widows

Ryan S. O'Connor[1] and Gary Ritchison[1,2]

ABSTRACT.—Because of their cryptic plumage and nocturnal habits, little is known about the breeding behavior of Chuck-will's-widows (*Antrostomus carolinensis*). Using temperature loggers and video-recordings, we quantified the incubation, brooding, and provisioning behavior of male and female Chuck-will's-widows in Adams County, Ohio, in 2011 and 2012. We located six nests, all 2-egg clutches laid on the ground. Four nests were successful, one was depredated, and one was abandoned. We quantified incubation behavior at all nests (mean = 5.5 days; range = 0.4–12.9 days). Adult Chuck-will's-widows incubated an average of 89.2% of the time, with females observed incubating more than males. Most incubation off-bouts (n = 104) occurred at dawn (0400–0659; n = 45) and dusk (1900–2200; n = 48) and averaged 35 mins in duration. After hatching, the mean duration of brooding bouts was 20 mins (age of young = 1–7 days). Both males and females provisioned young, and feeding rates were highest (P = 0.003) during the hour immediately after sunset. The timing of off-bouts during incubation and provisioning visits after hatching suggests that Chuck-will's-widows in our study foraged primarily at dawn and dusk. Previous authors have noted that nightjars are visual predators and, therefore, their foraging behavior may be constrained by light levels. *Received 24 January 2013. Accepted 23 April 2013.*

Key words: *Antrostomus carolinensis*, caprimulgids, iButton, nests, Ohio, off-bouts, on-bouts.

Nightjars and nighthawks (Family Caprimulgidae) are cryptically colored ground-nesters typically found in forested landscapes (Vilella 1995). Because of their cryptic plumage and nocturnal habits, little is known about their breeding behavior and most published information is based on qualitative, anecdotal accounts (e.g., James and Neal 1986, Peterjohn and Rice 1991, Palmer-Ball 1996). Among caprimulgids, incubation is thought to be primarily or exclusively by females (Vilella 1995), but males may occasionally incubate eggs during the day (e.g., Berry 1979). Incubation by Chuck-will's-widows (*Antrostomus carolinensis*) is thought to be primarily by females, but some cases of male incubation have been observed (Stevenson and Anderson 1994). Available information suggests that male Chuck-will's-widows may not provision or otherwise care for young after hatching (Ganier 1964, Stevenson and Anderson 1994, Straight and Cooper 2012).

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Clearly, additional studies are needed to better understand the breeding behavior of caprimulgids in general and Chuck-will's-widows specifically. Thus, our objectives were to quantify patterns of incubation and brooding behavior (e.g., duration of on-bouts vs. off-bouts) and examine the roles of males and females in provisioning young.

METHODS

Field work was conducted from 7 May–1 August in 2011 and 2012 at the Richard and Lucile Durrell Edge of Appalachia Preserve (hereafter, the Edge; 38° 45′ N, 83° 27′ W), Adams County, Ohio. The Edge encompasses about 5,665 ha and consists of mixed hardwood forests interspersed with open prairies and barren rocky outcroppings.

To locate potential nesting habitat (i.e., areas with dense cover near roads for forest edges; Straight and Cooper 2012), we used an aerial photograph to locate openings with mixed forest edges. From 7 May–15 June (2011 and 2012), we visited each area ($n = 26$) and delineated a series of transects 2 m apart and walked slowly along those transects searching for nesting adults. The number and distance of transects varied with the size of each area. For additional details concerning search methods, see O'Connor (2013).

When a nest was located, we noted the number of eggs and then checked nests every 1–4 days to monitor their status. When an adult was flushed from a nest, we noted its sex. Sex was determined by observing the outer rectrices; males have white outer rectrices and females do not (Pyle 1997).

Breeding Behavior and Nest Fate.—To examine incubation behavior, we simultaneously measured nest temperatures and ambient temperatures near nests using iButtons (Model DS1921G-F5#; Maxim, Sunnyvale, CA). iButtons were either placed at the base of eggs so that each side of an iButton was touching, almost touching, or in-between eggs. Using cyanoacrylate glue, we glued iButtons to the top of 7.5-cm-long metal screws and glued brown polyester fabric on top of the iButtons for camouflage. Screws were then pushed by hand into the soil until the iButton was flush with the ground (Hartman and Oring 2006). iButtons used to measure ambient temperature were randomly placed in the ground at least 5 m from nests. We programmed iButtons to record temperatures every 10 mins.

After young left nests or a nest failed, we retrieved iButtons and uploaded the temperature data as text files and converted them into Excel format (2007, Microsoft, Redmond, WA) where data were plotted on a line graph and analyzed visually (Hartman and Oring 2006). Patterns of incubation behavior (duration and timing of incubation on- and off-bouts) were determined by comparing ambient temperatures to nest temperatures, with a minimum off-bout change in temperature of 2.5 °C. Because iButtons only recorded temperatures every 10 mins, off-bout lengths could have been over- or underestimated by a maximum of 10 mins. For example, if a reading was taken at 0530 EDT with an adult on the eggs, the bird left at 0535, and then another nest reading was taken at 0540 with the adult still off the eggs, we would assume an off-bout of 10 mins based on the iButton data although the duration of the off-bout was actually 5 mins. Additionally, off bouts shorter than 10 mins may have been missed. To examine daily patterns of incubation behavior, we divided the day into four periods: dusk (1900–2200), night (2201–0359), dawn (0400–0659), and day (0700–1859).

To gather more detailed information about incubation behavior, nests were also monitored with video cameras (Model CCD-TRV138; Sony Corporation, Tokyo, Japan). During incubation, we videotaped nests every 2–4 days to limit disturbance to nesting adults. After eggs hatched, we typically videotaped nests or young every 1–3 days, with most videotaping during the period from 1800–0100. Cameras were mounted on tripods about 5 m from nests or young and recorded for 4 hrs.

Using video recordings, we quantified adult brooding and provisioning behavior. When possible, when subsequently reviewing videos, the sex of adults was determined by the presence (male) or absence (female) of white outer rectrices. Brooding was separated into two categories: (1) full brooding and (2) partial brooding. We defined full brooding as when both nestlings were under an adult's breast or abdomen. Partial brooding was when one nestling came completely out from under the adult's breast while the other nestling remained under. Provisioning behavior was quantified as the number of visits per 30-min interval. To determine if Chuck-will's-widows provisioned at higher rates during the periods prior to and after sunset, we created 30-min blocks of time spanning the period from 1700–0130. Each visit observed in videos was assigned to one of those blocks. Variation in feeding rates relative to time of sunset was examined using repeated measures

TABLE 1. Mean provisioning rates (visits to feed young/30 mins) of three pairs of Chuck-will's-widows (males and females combined) during 2011 and 2012 in Adams County, Ohio.

Time period[a]	Mean feeding rate	SE	n^b
31–240 mins before sunset	0	-	11
0–30 mins before sunset	0.6	0.4	5
0–30 mins after sunset	2.0	0.7	6
31–60 mins after sunset	1.8	0.3	4
61–90 mins after sunset	0	-	4
91–120 mins after sunset	0.5	0.3	4
121–270 mins after sunset	0	-	13

[a] Time 0 = time of sunset.
[b] Number of observation periods.

analysis of variance (SAS Institute 2004). Values are presented as means ± SE.

RESULTS

We located six nests (4 in 2011, 2 in 2012). All nests had clutches of two eggs laid on either leaf litter ($n = 4$) or bare ground ($n = 2$). Four nests were successful and two were not (one was depredated and one abandoned).

Using iButtons, we quantified incubation behavior for an average of 5.3 days at the six nests (0.4, 1.5, 3.2, 3.2, 10.7, and 12.9 days, respectively). Overall, adult Chuck-will's-widows incubated eggs 89.2% of the time (range = 76.7–93.3%). Incubation on-bouts averaged 442.1 ± 33.9 mins in duration ($n = 94$; females, $n = 12$ at four nests, males $n = 3$ at two nests, unknown adult $n = 79$; range = 2–970 mins). Female incubation bouts were longer (mean = 274.5 ± 82.9 mins, range = 11–897 mins) than those of males (mean = 7.7 ± 5.2 mins, range = 2–18 mins). In addition, during 16 visits to five nests to either change videotapes or iButtons, females flushed from nests more often ($n = 14$, or 87.5% of visits) than males ($n = 2$).

Most incubation off-bouts (93%) occurred at either dawn ($n = 45$ at six nests) or dusk ($n = 48$ at six nests); 10 off-bouts at five nests occurred during the night and one during the day (0741). The mean duration of off-bouts was 35.0 ± 3.9 mins (range = 1–280 mins, $n = 104$; by females $n = 12$, by males $n = 3$, unknown adult $n = 89$). The mean departure time of Chuck-will's-widows from nests at dusk was 16.9 ± 2.1 mins ($n = 49$) after sunset (range = 3 mins before sunset to 66 mins after sunset). At dawn, the mean time when adults left nests was 47.8 ± 4.2 mins ($n = 46$) before sunrise (range = 100 mins before sunrise to 89 mins after sunrise).

The brooding and provisioning behaviors of adult Chuck-will's-widows were monitored by videotaping at three nests when young ranged in age from 1–7 days. We analyzed 38.5 hrs of videos at these nests (6.5, 16, and 16 hrs, respectively), including 20.6 hrs during the period prior to and after sunset (1900–0130) and 17.9 hrs during the day. In addition, we approached nests with young ($n = 4$; range in age of young = 1–16 days) 18 times to check their status during the day ($n = 10$) and at dusk ($n = 8$), and found females with the young 16 times (88.9% of visits) and males twice (11.1%).

For males and females combined, the mean duration of full brooding bouts was 20.0 ± 3.5 mins ($n = 54$ at three nests, range = 6 secs to 118.7 mins). When the sex of brooding adults was known, the mean duration of brooding bouts was 23.9 ± 4.7 mins for females ($n = 37$ at two nests, range = 6 secs to 118.7 mins) and 4.9 ± 2.0 mins for males ($n = 8$ at two nests, range = 11 secs to 15.9 mins). Overall, the mean duration of partial-brooding bouts was 52 ± 6 secs ($n = 62$ at three nests, range = 8 secs to 4 mins). Mean duration of partial-brood bouts was 1.1 ± 0.3 mins for males ($n = 8$ at two nests, range = 8 secs to 2.9 mins) and 50 ± 7 secs for females ($n = 43$ at two nests, range = 9 secs to 4 mins).

During the period prior to and after sunset, feeding rates differed significantly among 30-min time blocks ($F_{6,10} = 7.8$, $P = 0.003$), with rates highest during the two 30-min periods just after sunset (Table 1). Overall, we observed 23 feeding visits, with eight by males, three by females, and 12 by adults of undetermined sex. In videos recorded during the day, we observed no feeding visits. However, an adult was always present with young during the day.

After hatching, young moved from nest sites ($n = 4$) on days 2, 2, 3, and 5 days post-hatching

(mean = 3.0 ± 0.7 days), respectively. At two nests, young moved farther from nest sites with increasing age; young were located 30 m from the nest site 10 days after hatching at one nest and 62 m from the nest site 16 days after hatching at a second nest.

DISCUSSION

Clutch Sizes.—All clutches of Chuck-will's-widows in our study consisted of two eggs laid on either leaf litter or bare ground. Although clutch sizes of Chuck-will's-widows can range from one to four eggs (Cleere 1999), Straight and Cooper (2012) reported that 95% of Chuck-will's-widow egg sets and nest records (n = 353) were two-egg clutches. Among caprimulgids, clutch sizes are generally either one or two (Cleere 1999). Other investigators have also reported that Chuck-will's-widows typically lay eggs on a substrate of pine needles, dead leaves, or bare ground (Hoyt 1953, Ganier 1964, Cleere 1999, Straight and Cooper 2012).

Incubation.—Although both male and female Chuck-will's-widows incubated eggs, our observations suggest that females spent more time incubating than males. We could only confirm that males (n = 2) briefly covered eggs on three occasions. Although additional study is clearly needed, these observations suggest that males may not actually incubate (i.e., apply heat to eggs), but may simply guard eggs while females are away. In support of this hypothesis, male Chuck-will's-widows do not have brood patches (Pyle 1997). Similarly, male Common Nighthawks (*Chordeiles minor*) do not have brood patches, and incubation is usually only done by females (Brigham et al. 2011).

During incubation, our observations suggest that female Chuck-will's-widows remained on eggs throughout most of the day and night. Straight and Cooper (2012) suggested that adult Chuck-will's-widows are reluctant to flush because their white eggs are obvious against the brown leaf litter. In addition, by incubating eggs throughout most of the night when temperatures are cooler, Chuck-will's-widows may be ensuring proper embryonic development.

Most incubation off-bouts in our study occurred at dusk and dawn, with eggs typically left unattended for about 35 mins per off-bout. Eastern Whip-poor-wills (*Antrostomus vociferus*) and Common Poorwills (*Phalaenoptilus nuttallii*) have also been reported to leave eggs unattended at dawn and dusk when adults exchange incubation duties (Cink 2002, Woods et al. 2005). Villela (1995) reported that Puerto Rican Nightjars (*Antrostomus noctitherus*) left eggs unattended at dawn and dusk, often for more than an hour. Nightjars are visually oriented crepuscular or nocturnal insectivores (Woods and Brigham 2008), so eggs are likely left unattended at dusk and dawn so adults can forage.

Brooding and Feeding Young.—Both male and female Chuck-will's-widows in our study brooded young after hatching, with males spending less time brooding than females. Although based on only eight observations at just two nests, male Chuck-will's-widows in our study were only observed brooding during short bouts at dusk after feeding young. Little is known about the brooding behavior of other caprimulgids. Brigham et al. (2011) indicated that only female Common Nighthawks brooded during the day, but provided no information about brooding at night. Woods et al. (2005) reported that both male and female Common Poorwills brood, but provided no details concerning the contributions of each sex. Similarly, Cink (2002) indicated that both male and female Eastern Whip-poor-wills brood young, but provided no information concerning the relative contributions of each sex. The brooding behavior of Lesser Nighthawks (*Chordeiles acutipennis*) appears comparable to that of Chuck-will's-widows in our study, with females doing most of the brooding and males brooding only briefly during feeding visits (Latta and Baltz 2012).

Both male and female Chuck-will's-widows fed young. We observed the highest feeding rates during the 60-min period immediately after sunset and adults were not observed provisioning young during the periods 31–240 mins before sunset or 121–270 mins after sunset. Although we did not videotape Chuck-will's-widows at dawn, Sprunt (1954) noted that they forage most often at both dusk and dawn. Nightjars are visual predators, and their foraging behavior may be constrained by light levels (Mills 1986, Bayne and Brigham 1995). Furthermore, the greatest amount of insect biomass may be available at dusk and dawn (Jetz et al. 2003).

Development of Young.—Within two days of hatching, young Chuck-will's-widows began moving from nest sites. Similar observations have been reported for other caprimulgid species (Villela 1995, Cleere 1999, Aragonés 2003). Hoyt (1953) found young 3 m from a nest site one day after hatching and 7.6 m away 3 days after hatch. Ganier (1964) found young Chuck-will's-widows 9.1 m from a nest site 5 days after hatching.

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Clutch Sizes, Fledging Success, and Nest-site Characteristics of Sharp-shinned Hawks in Kentucky

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ABSTRACT.—Because Sharp-shinned Hawks (*Accipiter striatus*) are among the most secretive of North America's forest-breeding raptors, little is known about their breeding biology, including the characteristics of their nesting habitat. In 2009 and 2010, we searched forest stands in Kentucky and located 11 nests, all in pines (*Pinus* spp.). Nests were at a mean height of 18.6 ± 1.4 m in trees with a mean height of 23.7 m. Comparison of the characteristics of nest sites and

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randomly selected unused sites revealed significant differences ($P = 0.021$). Discriminant analysis revealed that six variables (foliage cover, mean tree height, basal area, percent deciduous canopy cover, distance from edge, and distance from road) permitted the best discrimination between used and random sites. Sharp-shinned Hawks nested in areas closer to edges and in areas with denser stands of taller conifers and denser understory. All nests were in stands of young (~25–50 years), even-aged conifers about 18–25 m in height. Nest sites were also closer to edges where stands of dense pines transitioned into areas with more, shorter deciduous trees and less foliage cover than nest sites. These adjacent areas may provide better foraging habitat for nesting Sharp-shinned Hawks because small birds, their primary prey, are more abundant in mixed stands than in dense stands of conifers where they nested. *Received 19 January 2013. Accepted 22 June 2013.*

Key words: *Accipiter striatus*, canopy cover, even-aged stands, foliage cover, foraging habitat, nest success.

Populations of Sharp-shinned Hawks (*Accipiter striatus*) in North America are thought to be relatively stable (Sauer et al. 2008), but little is known about their population status in specific portions of their breeding range (Bildstein and Meyer 2000). Because so little is known, assessing possible effects of forest management practices and habitat loss and degradation on their population status is currently not possible.

Based on few studies and small sample sizes, Sharp-shinned Hawks will apparently nest in most forest habitats, particularly those with at least some conifers. In Missouri, these hawks were found to nest in stands of oak-hickory (*Quercus-Carya*) and pine (*Pinus*) with high tree densities and basal area (Wiggers and Kritz 1991, 1994). In Wisconsin, Sharp-shinned Hawks tended to nest in denser forests with younger, shorter trees and more conifers than Cooper's Hawks (*A. cooperii*; Rosenfield et al. 1991). Successful management requires information concerning where and how many birds are breeding and their nesting habitat requirements. Thus, our objective was to quantify features of habitat important in selection of nest sites by Sharp-shinned Hawks in Kentucky.

METHODS

From April–July 2009 and March–June 2010, we searched for nests in counties in Kentucky where Sharp-shinned Hawks had previously been reported during the breeding season (Palmer-Ball 1996; S. Vorisek, pers. comm.; see Rankin 2011 for additional details concerning search methods). When searching for nests, we walked through forest stands (defined as an area where tree composition and height were similar) while scanning for nests. Once located, nests were monitored at least once per week either by direct inspection (for accessible nests) or using binoculars and spotting scopes from the ground. For nests we were able to access, we determined the number of eggs present and hatching success. Nests were defined as successful if at least one young fledged.

After young fledged or a nest failed, habitat characteristics of nest sites were quantified following a modified version of methods described by James and Shugart (1970; Table 1). A nest site was defined as a 16-m-radius (0.08-ha) circle centered on the nest tree. To compare used and unused sites, one randomly selected, unused site was selected in each breeding territory. Although the size of territories in our study was unknown, mean distances between nests of Sharp-shinned Hawks are generally at least 1 km (Bildstein and Meyer 2000). Assuming territory boundaries would be about halfway between nests, territories would have a radius of about 500 m. Thus, to select a random location that would likely be within a territory, we moved a randomly selected distance (≥150 and 480 m) in a randomly selected compass direction from nest trees and, at that point, selected a tree that could have potentially been selected as a nest site (i.e., diameter at breast height within 5 cm of the nest tree). Except for variables specific to nests, the same measurements were made at random sites and nest sites.

Multivariate analysis of variance (MANOVA) was used to compare the characteristics of Sharp-shinned Hawks' nests and those of unused sites. Variables most important in discriminating between used and unused sites were determined by a stepwise discriminant analysis (backward procedure). All analyses were performed using the Statistical Analysis System (SAS Institute 2004). Values are presented as means ± SE.

RESULTS

We found 11 nests, including six in 2009 and five in 2010. All nests were in conifers, with five in loblolly pines (*Pinus taeda*), four in eastern white pines (*P. strobus*), one in a shortleaf pine (*P. echinata*), and one in a pitch pine (*P. rigida*). Nests were in trees with a mean height of 23.7 ± 1.7 m (range = 14–30 m) and a mean dbh of 38.2

TABLE 1. Description and measurement procedure for habitat variables used to characterize nest sites of Sharp-shinned Hawks in Kentucky.

Variable	Description and procedure
Coniferous canopy	Percent of coniferous canopy cover[a]
Deciduous canopy	Percent of deciduous canopy cover[a]
Total canopy cover	Percent total canopy cover[a]
Foliage cover	Number of vegetation 'hits' (vegetation touching 3-m high pole), with pole placed at 5 equidistant points along each transect
Small shrubs	Number of small (<1.5 m height) shrubs in 0.08-ha plot
Large shrubs	Number of large (1.5–3 m height) shrubs in 0.08 ha plot
Mean vegetation height	Mean height of plants located at 5 equidistant points along each transect
Understory trees	Number of understory trees <10 cm dbh in 0.08-ha plot
Overstory trees	Number of overstory trees ≥10 cm dbh in 0.08-ha plot
DBH	Mean diameter (cm) of all trees (>3 m in height) in 0.08-ha plot
Mean tree height	Mean height (m) of all trees (>3 m in height) in 0.08-ha plot
Basal area	Basal area (m^2 within 0.08-ha plot; $dbh^2 \times 0.00007854$)
Distance to nearest road	Distance (m) to nearest gravel or paved road
Distance to nearest edge	Distance (m) to nearest abrupt change in habitat features

[a] Percentages based on 5 densitometer readings along each of four 16-m transects (in the four cardinal directions) that intersected at nest trees.

± 2.3 cm (range = 26–51 cm). Nests were located at a mean height of 18.6 ± 1.4 m (range = 12–26 m). Nest sites were in areas of mixed coniferous/deciduous forest, with 61.4 ± 8.4% of trees within 16 m of nest trees being conifers and 38.6 ± 8.4% deciduous. Mean canopy cover (conifers plus deciduous trees combined) was 77.6 ± 1.9%.

The mean number of eggs per nest was 3.6 (n = 5 nests; 4 with 4 eggs and 1 with 2). The mean number of eggs that hatched per nest was 2.6 (n = 5 nests; 4 of 4 eggs hatched in each of three nests, 1 of 2 eggs in one nest, and none of 4 eggs in one nest). We determined the fate (i.e., whether or not young fledged) of 9 of 11 nests, and at least one young fledged from 7 of those 9 nests (77.8%).

Characteristics of Sharp-shinned Hawks' nest sites and unused sites differed significantly (Wilk's $\lambda = 0.1$, $F_{13,69} = 5.8$, $P = 0.021$). Stepwise discriminate analysis revealed that six variables, including distance from road, distance from edge, foliage cover, mean tree height, basal area, and percent of deciduous canopy cover, permitted the best discrimination between used and unused sites. Classification analysis correctly categorized 88.9% (8 of 9) of randomly selected sites and 90.9% (10 of 11) of used nest sites. Compared to the randomly selected, unused sites, the nest sites of Sharp-shinned Hawks were located in areas closer to roads and edges, with denser stands of taller conifers, and denser understories (below 3 m; Table 2).

DISCUSSION

The mean clutch size of Sharp-shinned Hawks in our study was 3.6, but most clutches (four of five) consisted of four eggs. Clutch sizes of Sharp-shinned Hawks range from 3–8, but clutches of 4–5 eggs are typical (Bildstein and Meyer 2000). Mean clutch sizes reported at other locations include 4.3 in Utah (34 clutches; Platt 1976), 4.5 in Missouri (8 clutches; Wiggers and Kritz 1994), and 4.6 in Oregon (5 clutches; Reynolds and Wight 1978).

Of nine Sharp-shinned Hawks' nests in our study where the outcome was known, at least one young fledged from seven (77.8%). Nest success (defined as ≥1 young fledging) reported at other locations include 92% in Oregon (Reynolds and Wight 1978) and 59% in southern Quebec (Coleman 2001). Because few investigators have attempted to document the nesting success of Sharp-shinned Hawks, causes of nest failure are not well understood. However, Bent (1937) noted that nestling Sharp-shinned Hawks were sometimes preyed on by Cooper's Hawks (*A. cooperii*) and Northern Goshawks (*A. gentilis*).

All nests of Sharp-shinned Hawks in our study were in pines and, compared with unused sites, nest sites were in areas with denser stands of taller conifers and denser foliage cover, and were closer to roads and edges. Similarly, Wiggers and Kritz (1991) located 17 Sharp-shinned Hawks' nests in Missouri, and all were in pine trees located in

TABLE 2. Mean (± SE) characteristics of nest sites of Sharp-shinned Hawks and of randomly selected unused sites in Kentucky, 2009–2010. Variables that permitted best discrimination between nest sites and randomly selected, unused sites are in bold font.

Variable	Nest sites (n = 11)	Randomly selected, unused sites (n = 10)[a]
Distance to road (m)	**126.8 ± 24.6**	**156.5 ± 47.6**
Distance to edge (m)	**52.3 ± 14.2**	**70.6 ± 19.0**
Foliage cover (no. of 'hits')	**34.5 ± 7.4**	**23.7 ± 4.7**
Mean tree height (m)	**15.4 ± 0.7**	**12.7 ± 0.8**
Basal area (m^2/0.08 ha)	**2.17 ± 0.18**	**1.61 ± 0.14**
Canopy cover, deciduous (%)	**12.3 ± 4.3**	**37.5 ± 9.5**
Number of small (<1.5 m in height) shrubs	215.1 ± 68.1	173.9 ± 53.3
Shrubs of large (1.5–3 m in height) shrubs	61.5 ± 19.5	29.2 ± 8.6
Understory trees (dbh <10 cm)	12.7 ± 2.4	17.0 ± 3.5
Overstory trees (dbh ≥10 cm)	33.5 ± 3.6	21.9 ± 3.6
Mean vegetation height (cm)	41.1 ± 11.6	32.9 ± 6.7
Mean dbh (cm)	24.3 ± 1.7	22.0 ± 1.5
Total canopy cover (%)	78.5 ± 2.8	76.6 ± 2.5
Coniferous canopy cover (%)	51.4 ± 4.6	34.5 ± 9.5

[a] Except distance from edge where n = 9

stands of either short-leafed pine or mixed species of pines. In addition, as in our study, Sharp-shinned Hawks in Missouri nested in high density stands of pine trees that averaged 16.7 m in height (Wiggers and Kritz 1991). In New Mexico, nesting Sharp-shinned Hawks were also found in dense stands (basal area = ~38 m^2/ha; canopy cover = ~78%) of ponderosa pine (*P. ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and white fir (*Abies concolor*; Siders and Kennedy 1996). Similar results, with Sharp-shinned Hawks nesting in young, even-aged stands of conifers, have been reported in Oregon (Reynolds et al. 1982) and Wisconsin (Trexel et al. 1999). Although Sharp-shinned Hawks will nest in deciduous trees (Bildstein and Meyer 2000), our results and those of previous studies suggest that conifers are more often used as nest sites, particularly conifers located in stands of young (~25–50 years), even-aged conifers about 15–20 m in height. Reynolds et al. (1982) suggested that dense vegetation may provide cover and protection from nest predators.

Nest sites of Sharp-shinned Hawks in our study were closer to edges than random sites, with edges representing areas where nest stands (i.e., dense stand of pines) transitioned into areas with fewer conifers, more deciduous trees, and less foliage cover. Because the ranges of Sharp-shinned Hawks can extend >1 km from nest sites (Platt 1973, Reynolds 1979), these areas were likely within the ranges of hawks in our study. Other investigators have also noted that nest sites of Sharp-shinned Hawks may be adjacent to clearings, brushy areas, or open deciduous forest (Palmer 1988). Such areas may provide better foraging habitat because small birds, the primary prey of Sharp-shinned Hawks, may be more abundant in mixed stands than in dense stands of conifers (Palmer 1988). Thus, when choosing nest sites, Sharp-shinned Hawks may prefer areas with dense stands of conifers that provide nest sites, but with adjacent areas within 1–1.2 km consisting of mixed stands of forest where more potential prey may be available.

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Interspecific Parental Care by a Wood Thrush (*Hylocichla mustelina*) at a Nest of the Veery (*Catharus fuscescens*)

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ABSTRACT.—Reports of interspecific parental behavior are rare but widespread among avian taxa. We present the first known case of interspecific parental care by a Wood Thrush (*Hylocichla mustelina*) at a nest of the Veery (*Catharus fuscescens*), documented by video at a long-term study site in northern Delaware, USA. We provide data on nest chronology, quantify parental behavior, and describe a copulation event between the Wood Thrush and the female Veery that was captured on video. Despite incurring no obvious fitness benefit, the Wood Thrush provided significant and prolonged nestling care including more feeding attempts and sanitation maneuvers than either Veery. We propose that these observations are a consequence of the normal adaptive behavior of the recipient species. *Received 27 March 2013. Accepted 29 July 2013.*

Key words: *Catharus fuscescens*, *Hylocichla mustelina*, interspecific parental care, Veery, Wood Thrush.

Reports of interspecific parental care, when an adult of one species provisions the offspring of another, are rare yet sufficiently widespread among avian taxa so as to beg an explanation (Shy 1982, Skutch 1987). Proposed explanations have focused on the proximate cause of the helper's behavior with the assumption that interspecific parental care is not adaptive to the helper because it confers no direct or inclusive fitness benefit (Brown 1983, 1987). Thus, interspecific parental care in birds is generally assumed to be a rare mistake (e.g., Schaeffer et al. 2009).

Here, we quantify interspecific parental care at a nest of the Veery (*Catharus fuscescens*) at a long-term study site in Delaware. The nest was attended by two adult Veeries (one female, one male) and a male Wood Thrush (*Hylocichla mustelina*). We compare the parental contribution of the heterospecific helper with the care given to the nestlings by the conspecific parents. We examine proximate reasons posited by Shy (1982)

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to explain interspecific nestling care and present an alternative explanation that integrates the potential benefit incurred by the recipient species as a partial explanation for these events. We also describe a copulation event between the Wood Thrush and the female Veery. Of note, *Catharus* and *Hylocichla* are sister genera that have been the focus of taxonomic debate for more than half a century (e.g., Ripley 1952, Dilger 1956, Hendrickson and Yow 1973, Winker and Rappole 1988, Winker and Pruett 2006).

METHODS

Our observations occurred May–June 2011 at a long-term study site at White Clay Creek State Park, New Castle County, Delaware (39° 44′ N, 75° 45′ W). CMH has been monitoring nests of Veeries at this site since 1998 (e.g., Heckscher 2004, Halley and Heckscher 2012). The nest of interest was constructed within 1 m of the ground in a dense shrub, *Rosa multiflora*. The nest was discovered on 25 May by following a female Veery with nest material, and its status was subsequently monitored via digital video (model ATC2K, Oregon Scientific, Tualatin, Oregon, USA) and direct observation until 20 June, by which time all four offspring had fledged. Both adult Veeries had been banded in previous years, each with a unique combination of three colored bands and one numbered aluminum band (Bird Banding Laboratory, USGS Patuxent Wildlife Research Center, Patuxent, Maryland, USA). We banded the four nestlings on 17 June, but the Wood Thrush was neither captured nor banded.

The first egg was laid on 28 May. The clutch had increased to three eggs by 0700 EDT (Eastern Daylight Time) on 30 May, at which time we deployed the video camera. Footage showed the female incubating regularly as of 30 May. Three eggs were seen in the nest at 0806 on 31 May. A fourth egg was found in the nest at 0645 on 1 June, at least 2 days after the onset of incubation. Two eggs hatched on 9 June, and a third on 10 June. Normal incubation length in our population is 12 days (CMH, unpubl. data), and the fourth egg hatched on the expected date of 13 June. Throughout the nestling period, the nestling that hatched from the fourth egg (hereafter "runt") was easy to distinguish from its siblings because of its noticeably smaller size. During the banding session on 17 June, the pin feathers of the runt were still unbroken 2 days after the feathers of its siblings had emerged. The first fledging event was captured on video at 1614 on 19 June. Two more young fledged before the next video session, and the fledging of the runt was captured on video at 1010 on 20 June. The calls of two offspring (the first to fledge and the runt) were captured by the camera microphone; both birds uttered the two-syllable "*v-shaped* call" of the Veery fledgling call repertoire (Fig. 1; Heckscher 2007).

In the laboratory, we reviewed video footage with Windows Movie Maker software (version 6.0, Microsoft Corporation, Redmond, Washington, USA). Morning video sessions ($n = 4$) were initiated in the field between 1013–1017. Footage captured prior to 1030 was truncated during analysis to mitigate the potential effect of researcher presence on parental behavior and to standardize start times. A single evening video session on 19 June was initiated at 1613 and truncated to 1630 during analysis. Each video session was sampled for 3 hours, yielding a total of 15 hrs of video footage for analysis. The identities of individual nestlings were discernible in video footage following their banding date (17 June). For all post-banding sessions ($n = 3$), parental contributions to individual nestlings were tallied. We quantified (1) the number of food deliveries intended for each nestling (i.e., the intended target of the food delivery based on the initial movement of the adult feeder upon arrival at the nest, regardless of whether nestlings usurped one another), and (2) the number of fecal sacs removed or injested from each nestling. Results were analyzed with Excel and Minitab 16 software (Microsoft Corporation, Redmond, Washington, USA). We used a Chi-square goodness of fit test to examine whether the delivery of food and the removal of fecal sacs were random in relation to individual nestlings and the adults that delivered/removed them. All errors are reported as ± 1 standard deviation.

RESULTS

All four offspring were provisioned by three adult birds: (1) a banded female Veery, ≥3 years of age, (2) a banded male Veery, ≥2 years of age, and (3) an unbanded Wood Thrush of unknown age. Both Veeries were detected feeding in all video sessions, but the Wood Thrush was not detected until 16 June (Fig. 2). During video sessions III–V, after the Wood Thrush first appeared at the nest and during which the identities of individual nestlings were discernible,

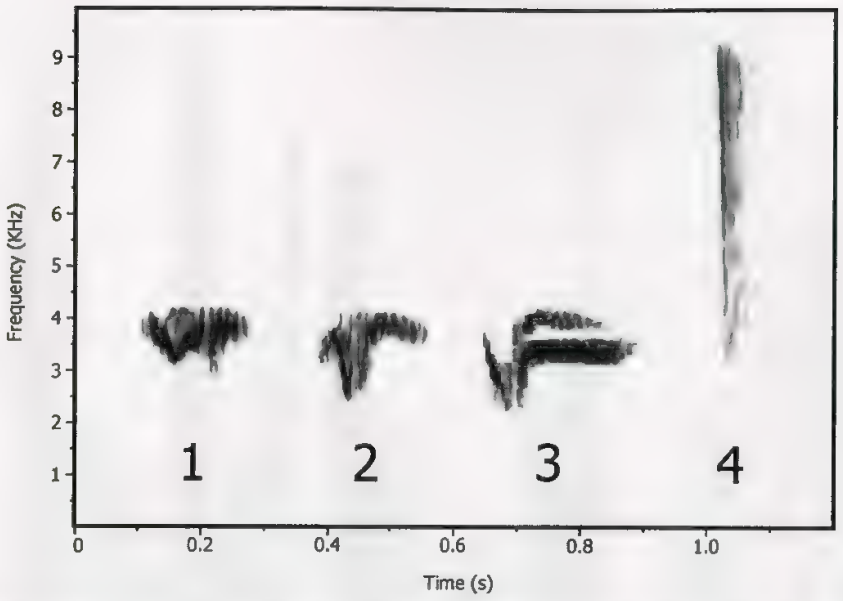

FIG. 1. Three *v-shaped* calls of Veery fledglings from White Clay Creek State Park, New Castle County, Delaware, and a call of a Wood Thrush fledgling from Montgomery County, Pennsylvania: (1) first fledged young from the present study, (2) fourth fledged young from the present study ("runt", see text), (3) *v-shaped* call from the Veery fledgling vocal repertoire shown for comparison (from Heckscher 2007), and (4) a comparable call (recorded by Paul Driver in Jun 2012) from a Wood Thrush fledgling.

the Wood Thrush delivered food 78 times to the nestlings, compared to 33 and 15 deliveries by the female and male Veeries, respectively ($\chi^2 = 49.8$, df = 2, $P < 0.001$; Fig. 2). During sessions III–V, the Wood Thrush disposed of more fecal sacs ($n = 26$) than either the female ($n = 18$) or male ($n = 6$) Veery ($\chi^2 = 11.2$, df = 2, $P = 0.003$), but no individual nestling was favored ($\chi^2 = 0.38$, df = 3, $P = 0.9$). Food deliveries by the three adults were not distributed evenly among the four offspring ($\chi^2 = 33.5$, df = 3, $P < 0.001$; Fig. 3). The Wood Thrush fed the runt significantly more than its siblings ($\chi^2 = 31.51$, df = 3, $P < 0.001$; Fig. 3). Similarly, the female Veery's propensity to favor food delivery to the runt, compared to the other nestlings, was nearly significant ($P = 0.06$; Fig. 3). The male Veery did not favor any particular nestling ($P = 0.9$; Fig. 3). The male Veery's feeding rate appeared to decline progressively as the nestlings approached fledging (Fig. 2).

In video footage captured at 1135 on 16 June, the female Veery and Wood Thrush were simultaneously present at the nest and both birds delivered food to the nestlings. Subsequently, the Wood Thrush mounted the female Veery, after which the female left the nest (Fig. 4). The Wood Thrush followed the female (offscreen) with fluttering wingbeats, as observed after other Wood Thrush copulation events (CMH, unpubl. data).

DISCUSSION

After its initial appearance, parental care provided by the Wood Thrush exceeded that of both adult Veeries. The Wood Thrush provided significantly more food deliveries and sanitation maneuvers than either Veery. We are not aware of other studies of interspecific parental care in wild passerines that have quantified the contribution of the heterospecific helper in relation to the nest owners. Thus, this study of interspecific parental behavior is perhaps the most detailed of any observation of its kind and precludes quantitative comparison to other studies. Most reports of interspecific parental behavior in passerines are limited to brief anecdotal accounts (e.g., Skutch 1935, 1961, 1987; Shy 1982). In an aviary, an unmated Wood Thrush fed the offspring of several species including Veeries (Skutch 1961), and Schaeffer et al. (2009) described a wild nest of a Wood Thrush that was attended by a male Eastern Towhee (*Pipilo erythrophthalmus*), but neither a wild Wood Thrush rearing heterospecific

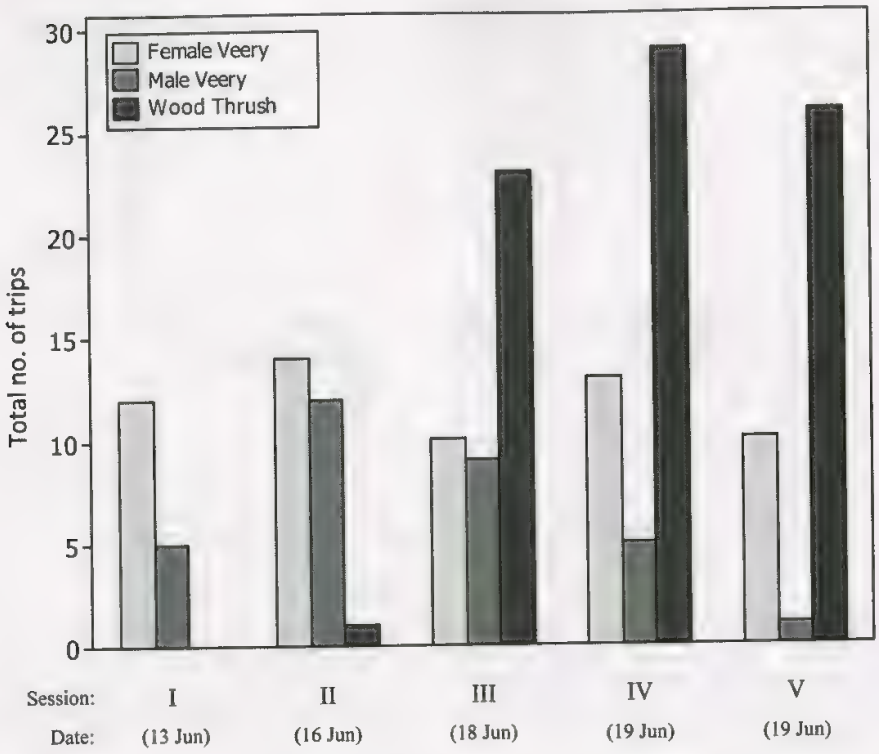

FIG. 2. Total number of trips for each of five 3-hr video sessions (I–V) at a nest of the Veery (*Catharus fuscescens*) that was attended by two conspecifics and a Wood Thrush (*Hylocichla mustelina*) in Delaware. Sessions I–IV were initiated at 1030 EDT and session V was initiated at 1630.

offspring, nor interspecific parental care at a wild nest of a Veery, have been reported.

Shy (1982) classified reports of interspecific parental care according to proximate, non-mutually-exclusive causes: (1) the nest contained offspring from both species (i.e., a mixed brood), (2) the helper's own nest was destroyed, (3) the helper's nest was in close proximity to the recipient nest, (4) the helper was attracted to the recipient nest by nestling vocalizations, (5) the recipient offspring were orphaned and later adopted by the helper, (6) the helper (male) fed the recipient offspring while his mate incubated, (7) the helper was unmated, (8) some other reason – the largest category, representing 26.5% of total cases. Although we cannot rule out all of the above proximate causes for the Wood Thrush's behavior, we do not believe the nest contained Wood Thrush young (i.e., mixed brood) or hybrids for the following reasons: (1) two of the four young, including the runt that was disproportionately provisioned by the Wood Thrush, emitted the *v-shaped* call characteristic of Veeries at the time of fledging, whereas the fledgling Wood Thrush call is a rapid single-syllable *chip* (Fig. 1; Evans et al. 2011), and (2) we have observed hundreds of Veery nestlings since the implementation of this long-term study, and there was no discernible departure from typical plumage of Veery nestlings among this brood.

At our study site, the nests of some female Veeries are attended by multiple male Veeries, and males may feed at multiple nests in a single season, each attended by a different female (Halley and Heckscher 2012). In this system, some female Veeries may benefit by augmented parental support, and perhaps by securing insurance against desertion from polygamous males, while males may benefit by maximizing the number of young they sire. In the polygynandrous Dunnock (*Prunella modularis*), females recruit multiple males by copulating with them (Davies 1985, 1986) and males of the polygynandrous Alpine Accentor (*Prunella collaris*) will only attend nests if they have copulated with the female owner (Nakamura 1998a, b). Similar behavior is reported for other species that practice cooperative polyandry (e.g., Tasmanian Native-hen

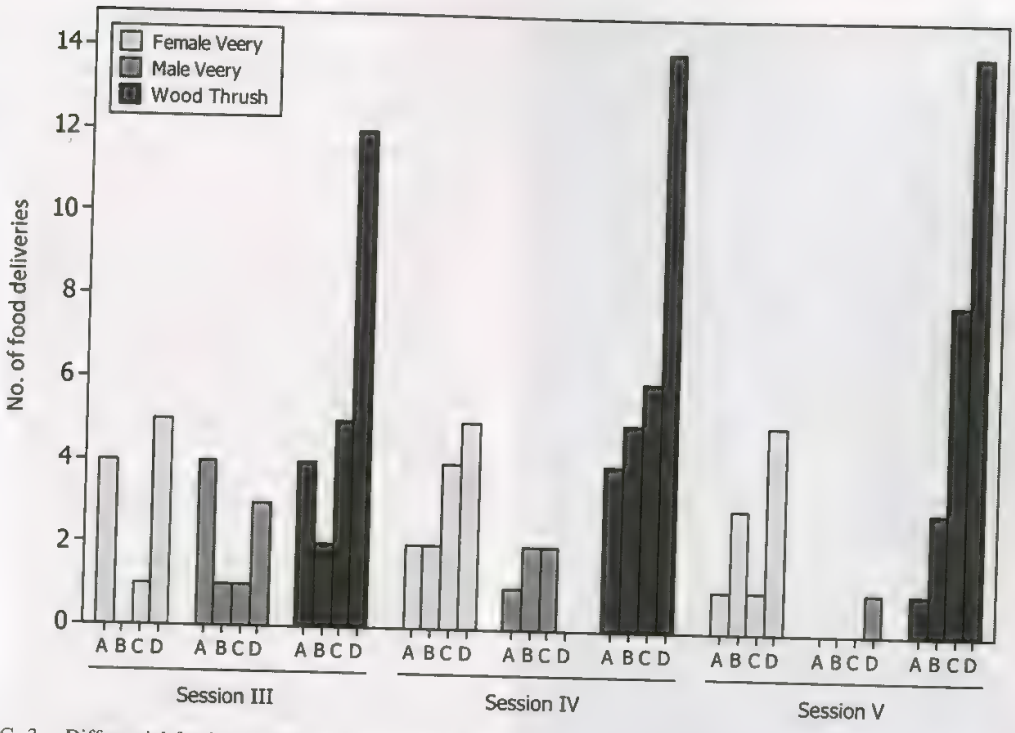

FIG. 3. Differential food deliveries to four offspring (A–D) by two adult Veeries (*Catharus fuscescens*) and a Wood Thrush (*Hylocichla mustelina*) at a Veery nest in Delaware. The allocation of food items among individual nestlings was determined by recording the intended target of each food delivery (i.e., initial movement of the adult feeder), regardless of whether the nestlings subsequently fought over food. Nestling D was designated as the runt (see text).

[*Tribonyx mortierii*], Maynard Smith and Ridpath 1972; Galapagos Hawk [*Buteo galapagoensis*] Faaborg et al. 1980; Purple Swamphen [*Porphyrio p. melanotus*] Craig 1980). We do not know whether female Veeries recruit helpers in this manner, but if they do, the interspecific parental behavior documented in this study may be the consequence of a female Veery inadvertently recruiting a Wood Thrush rather than a second Veery. Thus, the Wood Thrush's parental investment might be the normal reaction of a male that has copulated with a receptive female, albeit one of a different species. Although the two species differ in some key behavioral traits such as breeding phenology and the use of vocal repertoires (e.g., Brown and Roth 2002, Heckscher 2007), various phenotypic similarities such as morphology and shared postural displays (Dilger 1956, Winker and Rappole 1988) may render the Wood Thrush susceptible to sexual solicitation by a Veery. If so, the interspecific parental behavior exhibited here might be a consequence of the normal adaptive behavior of the recipient species.

Shy's (1982) proximate causes were considered environmental stimuli that may have induced nonadaptive behavior in the heterospecific helper. Notably, Shy (1982) did not suggest that the adult behavior of the recipient species might be a proximate mechanism leading to interspecific parental care. In light of the copulation event and the significant parental care exhibited by the Wood Thrush, we suggest that sexual solicitation by the female Veery could have prompted the interspecific helping behavior of the Wood Thrush. Future study of breeding behavior in the Veery and its polygynandrous congener Bicknell's Thrush (*C. bicknelli*; Goetz et al. 2003) may clarify the means by which females of these secretive species recruit multiple male feeders, and allow for a more robust assessment of our hypothesis.

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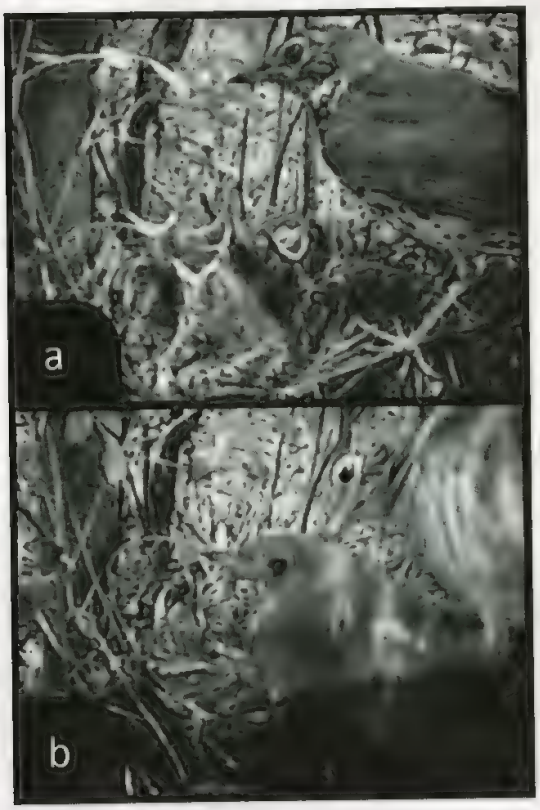

FIG. 4. Still images from a video recording of a Veery (*Catharus fuscescens*) nest in Delaware attended by a Wood Thrush (*Hylocichla mustelina*): (a) the Wood Thrush at the nest just after food delivery, and (b) the Wood Thrush mounting the female Veery.

recording of a Wood Thrush fledgling call presented in Fig. 1. L. Lester and two anonymous reviewers provided insightful comments that improved the manuscript. We are grateful to N. McFadden, C. Bennett, and the staff of White Clay Creek State Park and the Delaware Division of Parks and Recreation for their cooperation.

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Ecological Constraints and Phenotypic Accommodation in One-legged Eared Grebes

Joseph R. Jehl, Jr.[1]

ABSTRACT.—An Eared Grebe (*Podiceps nigricollis*) that lost a leg in an accident increased muscle mass in its intact leg by 28%. This allowed it to forage, run along the surface to take flight, and survive for about a year before dying in a weather-induced downing. Its ultimate survival probably depended on the species' predilection for hypersaline habitats, where passive invertebrates are abundant and can be captured easily on the surface without the need to dive. Similar phenotypic accommodation may have been realized in other similarly impaired Eared Grebes. However, it seems unlikely to be achieved in other grebe species, particularly fish-eating pursuit divers, which require two intact legs and feet for propulsion and underwater maneuverability. *Received 14 February 2013. Accepted 14 June 2013.*

Key words: Eared Grebe, ecology, phenotypic flexibility, *Podiceps nigricollis*.

Understanding the manner and degree by which organisms are able to accommodate physically to environmental change without further genetic change is a central issue in studies of ecological development (''eco-devo''; e.g.,West-Eberhard 2003, Sultan 2007, Piersma and van Gils 2011). One source of insight into the limits of this so-called phenotypic accommodation (phenotypic flexibility, adaptive plasticity) comes from accidental injuries or developmental anomalies, the latter exemplified by Slijper's (1942a, b) classic study of a goat born without forelimbs that adopted a bipedal existence.

In birds the loss of both legs is inevitably fatal–an outcome initially unappreciated for the Birds of Paradise, which were once fancied by 16th century naturalists to have a completely aerial existence because the legs (and sometimes wings) of the first specimens to reach civilization had been removed in preparation (the type species of the genus *Paradisaea* is *apoda*). In some taxa (e.g., shorebirds, gulls, blackbirds), it is not unusual to encounter individuals that have lost a single leg or foot to accident or disease, and that are able to cope for at least short periods. However, for foot-propelled divers such as grebes, which require strong legs and feet not only to swim and maneuver underwater but also to run across the surface in order to take flight, such a challenge to adapt phenotypically would seem so insurmountable that afflicted individuals would be quickly selected out of the population. Or wouldn't they?

On the evening of 12–13 December 2011, an estimated 30,000–50,000 Eared Grebes (*Podiceps nigricollis*) departed Great Salt Lake, Utah, en route to wintering areas in Mexico or southern California (Jehl et al. 2012). After several hours some became disoriented in a snowstorm and >7,000 crashed near Cedar City, Utah. Because grebes are unable to take off from land, local authorities rescued several thousand and transported them to open water from which they might continue their migration. At least 3,000 were killed outright. Included in a subsample ($n = 101$) donated to the U.S. National Museum of Natural History was a bird that differed in three notable ways: (1) it was the only one in the group (or in a photographic sample of salvaged and released) that had not completed prebasic molt; (2) at 347 g, it was by far the smallest , weighing 53 g less than the next lightest male and 77 g (18%) less than the mean (Table 1); and (3) it appeared to be legless. Subsequent CT scans showed that the right tibiotarsus had been fractured in the crash and the lower leg snapped off at the ankle. The lower left leg, however, was indeed missing and consisted of only a well-healed stub enclosing the proximal 14.2 mm of the tarsometatarsus (Fig. 1A). Smooth and rounded edges of the included bone fragments showed that the injury was of long standing.

The grebe (USNM no. 623675, flat skin and skeleton) was a male. Plumage characters, soft part coloration, and juvenal primaries that had not been replaced through the second fall staging period established its age at about 17 months (Storer and Jehl 1985). The entire skeleton was

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TABLE 1. Body composition (g) of a one-legged Eared Grebe (USNM 623675) compared with adult males downed in the same flight.

Component	One-legged grebe	Other males (range, mean ± SD; $n = 5$)
Body	347	400–490 (432 ± 22) [a]
Breast (one side)	Left, 22.57 (damaged, incomplete); Right, 24.47	23.2–25.6 (24.0 ± 0.6)
Leg	Left,11.21; Right, 20.96	14.4–17.2 (16.4 ± 1.1)
Entire stomach	11.8	7.6–10.7 (9.42 ± 0.12)
Liver	6.8	6.3–9.6 (7.64 ± 0.15)
Fat[b]	100.2	159.4

[a] $n = 38$
[b] Calculated ; J. Jehl and H. Ellis unpubl.

badly damaged. Elements that remained intact (humerus, ulna, radius, coracoid, femur), external measurements (bill, wing), and testis size (4 × 2 mm) were similar in size to those of other downed males. Extensive internal damage made it impossible to determine the size and configuration of individual muscles in either leg, except to note that those in the injured leg had atrophied, whereas those in the intact leg were twice as large and had hypertrophied to 28% greater than average. No other asymmetry was evident, except that the left tibiotarsus was slightly less robust at its base and the trough of the cnemial crest was slightly narrower.

Knowledge of the natural history of Eared Grebes (reviewed in Cullen et al. 1999, Jehl et al. 2003) allows inferences about the past of this individual and how it adapted behaviorally to its injury. After leaving fresh water breeding habitats, Eared Grebes typically move promptly to hypersaline lakes to molt, stage, and feed on the abundant invertebrate populations (Jehl et al. 2003, 2012; Jehl and Henry 2010). There, they become incapable of flight for months because of atrophy of the breast muscles and the acquisition of huge fat stores. When food is no longer accessible they rebuild breast muscle, reduce the size of the digestive organs, decrease body weight, and depart for saline wintering areas in Mexico or Southern California (Jehl 1997, 2007). In spring, the majority return north through the interior, with tens of thousands in most years stopping at the Salton Sea, California, before returning to breeding areas. On the breeding

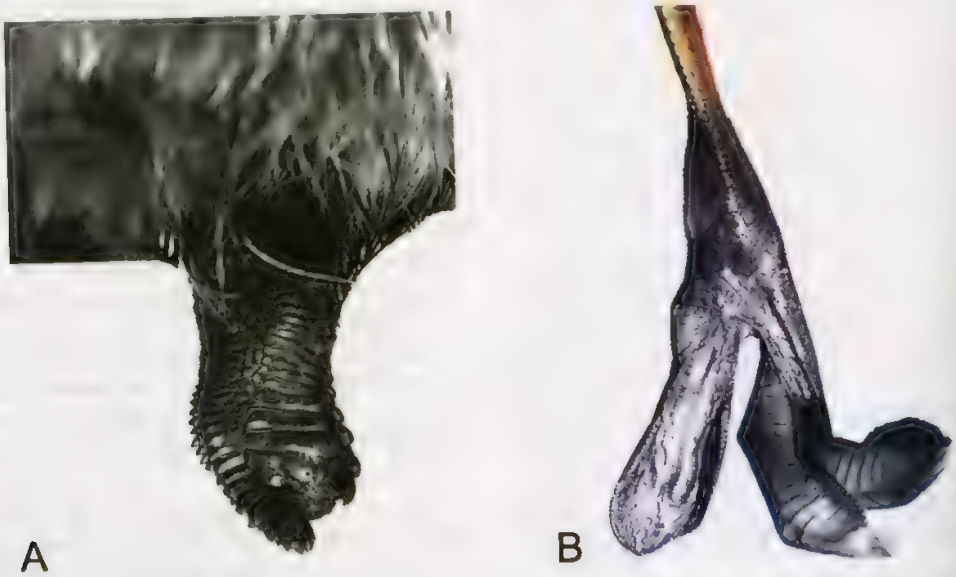

FIG. 1. A. Stump of the left leg of an adult Eared Grebe downed in post-staging migration in Utah, 11–12 December 2011. B. Deformed foot and inflexible twisted toes of an adult Eared Grebe staging at Mono Lake, California, 10 September 1995.

grounds grebes are mostly sedentary, but most stages of their migrations require several take-offs and landings, which are followed by prolonged stopovers (Jehl 1997, Jehl et al. 2003).

As the one-legged grebe was of average size and showed no significant asymmetry in its leg bones, I infer that it had no difficulty in getting food during its initial growth and that the injury probably occurred after it left the breeding grounds. The configuration of the injury, with the tarsometatarsus having been severed cleanly, is consistent with that expected of a fish or turtle bite. Since neither of those occurs in Great Salt Lake, I surmise that the loss occurred on the oceanic/Gulf of California wintering grounds when it was 6–8 months old. The immediate phenotypic accommodation would have been hypertrophy of muscles on the intact leg, which would allow it to swim at the surface, albeit with little directional control. Its diving ability had to have been greatly limited, as the loss of a leg–and a foot needed for maneuvering–would have precluded its typical feeding behavior of hovering in place underwater to glean invertebrates from the substrate or submerged rocks. However, Eared Grebes prey to a large extent on slow-moving invertebrates that can be pecked from the water surface (e.g., brine shrimp, brine flies; Cullen et al.1999), so obtaining food might not have been its major problem.

A greater issue was migration. Grebes must run for long stretches on the water to get airborne. This bird must have taken flight repeatedly during its first adult year to shift from wintering to breeding grounds in spring and then reach Great Salt Lake in fall. Taking off required a lopsided push from a hypertrophied leg coupled with wings beating on the surface. Although it had completed the spring molt into breeding plumage, its restricted mobility probably precluded participation in the vigorous surface displays and synchronized underwater swimming that are involved in pair formation (Konter 2012).

Leaving Great Salt Lake in fall, however, posed a challenge. Eared Grebes attain their maximum weight (>600 g) at this season, then lose weight when reorganizing body composition for flight (Jehl 1997). Adult males depart at about 450 g, of which 150 g is breast muscle and 160 g fat (Table 1). Breast muscle and other body components in the one-legged grebe were as expected in post-staging migrants, but at 347 g it was by far the lightest in its cohort and had only 100 g of fat. This, plus the delayed molt and the fact that its stomach was relatively large (expected of birds that are on short rations; Piersma and van Gils 2011, Jehl and Henry 2013), suggests that it fed poorly in the days before departure. An alternative possibility is that the bird was able to fatten normally early in the season but lacked sufficient leg power to get airborne until its weight had dropped to 350 g. In either case, its body condition would have been marginally sufficient–barring the snowstorm–to take it to wintering areas.

This one-legged Eared Grebe was not unique. Jehl et al. (1999) reported a one-footed bird captured for banding at Mono Lake, along with four others with impairments (club foot, dislocated ankle joint, deformed and twisted toes; Fig 1B) severe enough to prevent them from diving normally; indeed, it was the inability of most of these birds to submerge that led to their discovery. All were at or above normal weight (>400 g) for the time of capture in early September, when food was abundant at the surface. One would expect such birds to be eliminated late in the staging season when surface food was no longer available, a notion further supported by the lack of serious foot defects in >2,000 grebes killed in previous downings (Jehl et al.1999, J. R. Jehl et al., unpubl. data). Yet, at least three of the five banded birds were adults, and thus had survived at least one year. Also, in at least two of those cases the injuries were congenital, showing survival since hatching.

The significance of these severely impaired grebes, as with the two-legged goat and other "flexible monsters" (West-Eberhard 2003) lies not in their survival but in revealing how environmental factors constrain and shape the degree to which the phenotype can be restructured via adaptive plasticity. Here, a one-legged Eared Grebe survived by increasing muscle in its intact leg; whether the other impaired grebes exhibited similar plasticity was not studied. In all cases, however, the grebes' survival benefited by their extended residence at hypersaline lakes, where the abundance of surface invertebrates, absence of aquatic predators, and virtual lack of raptors, combine to promote very high survivorship in the fall staging period (Jehl 1988, Jehl et al.2002). These same environmental factors have been implicated in the Eared Grebe's status as the commonest grebe species in the world (Jehl 2001).

Although the potential for similar phenotypic accommodation likely exists in other grebe species, it seems unlikely to be realized. Other invertebrate-eaters, with few exceptions (e.g., *Tachybaptus ruficollis*), have little propensity for

surface feeding (see Fjeldså [2004] for details on foraging behavior) and few, if any, occupy habitats as salubrious as the hypersaline lakes preferred by Eared Grebes. And the pursuit divers (e.g., Western Grebe *Aechmophorus occidentalis*) require two strong legs to generate the speed needed to catch fish as well as large feet to provide the underwater maneuverability essential for capturing active prey. For them, life with but one leg is inconceivable. Or is it?

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Covey Membership and Size Dynamics in a Low Density Population of Northern Bobwhites

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ABSTRACT.—Northern Bobwhites (*Colinus virginianus*) are predicted to maintain optimal covey sizes throughout the non-breeding season to avoid predators, thermoregulate, and forage efficiently. Arguably, population declines that reduce local bobwhite population densities could influence coveying behavior, which may then affect individual survival and population growth rates. We investigated changes in covey size and membership in a declining bobwhite population on private land in southwestern Ohio. Covey densities (range 0.25–1.63 coveys/km^2) were lower than estimates from other areas of the bobwhite range. Despite an average 3.2% weekly decline in mean covey size during October–March, two unique coveys merged to form larger coveys on only six occasions and only one radiomarked individual changed covey affiliation (n = 307 radiomarked individuals, n = 57 coveys). Spatiotemporal separation of coveys and low daily movement rates (139.2 m/day) provided little opportunity for contact among adjacent coveys, possibly inhibiting mergers and inter-covey movements of individuals, particularly during winter. We postulate that low incidences of covey mergers and inter-covey movement by individuals were associated with spatial isolation of coveys because of low population densities on our study sites. Such density-dependent social structure would likely lower non-breeding season survival in low-density populations and therefore have implications for population viability. *Received 22 April 2013. Accepted 5 July 2013.*

Key words: *Colinus virginianus*, covey behavior, density, movements, Northern Bobwhite.

Northern Bobwhites (*Colinus virginianus*) form tight social groups during the non-breeding season (hereafter coveys; Johnsgard 1973) to improve individual thermoregulation (Case 1973), foraging efficiency, predator avoidance, and survival (Williams et al. 2003). Such social behavior is likely to have important implications for population-level demographics and may be sensitive to changes in population density (Courchamp et al. 1999, Liermann and Hilborn 2001) or habitat fragmentation (Cale 2003). Long-term range-wide population declines of bobwhites caused by land use change may have unanticipated influences on covey behavior and population dynamics. Such changes would be especially important in bobwhite populations near the northern extent of their range where the coveying period coincides with seasonally high mortality rates (Roseberry and Klimstra 1984) that have been shown to have a strong influence on population growth (Folk et al. 2007, Sandercock et al. 2008, Gates et al. 2012). Despite the potential influence of covey behavior in declining populations, few studies have addressed the significance of covey size and membership dynamics in populations across the bobwhite range.

Williams et al. (2003) found that covey size influenced individual survival, foraging behavior, and movement rates in aviary and field experiments in Kansas. Specifically, individual survival and foraging efficiency was highest in coveys near an optimal size (11 individuals) and declined in larger and smaller coveys. Because maintaining optimal covey size is an important determinant of individual survival (and ultimately fitness), we expect that individual bobwhites would move among coveys throughout the non-breeding season to maintain optimal group sizes. Additionally, individuals in suboptimal sized groups should either combine (in the case of small coveys) or split to maintain group sizes that maximize individual survival. The tendency for individuals to move among coveys throughout the non-breeding season and for small coveys to combine to form larger coveys has been well established in a number of natural history studies from more southerly areas in the core the bobwhite range where densities are higher (Stoddard 1931, Rosene 1969, Yoho and Dimmick 1972a, Lehmann 1984, Williams et al. 2004). However, a few studies of more northern populations with generally lower densities have reported little variation

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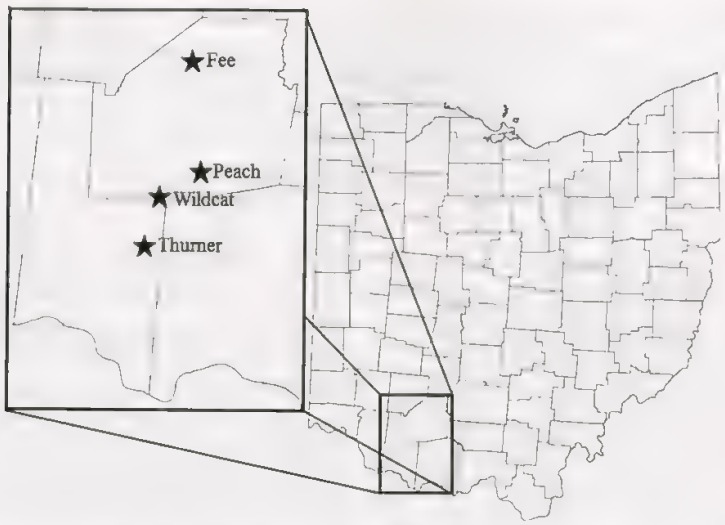

FIG. 1. Location of four private land study areas in southwestern Ohio on which we radiomarked coveys of Northern Bobwhites during October–March 2009–2011.

in covey affiliation of individuals during the non-breeding season (Murphy and Baskett 1952, Robel and Kemp 1997), though none have examined the implications of this behavior. Such variation among populations in different regions or at different densities may exert strong influences on local and regional population dynamics and viability (Cale 2003).

Bobwhite populations were historically widespread throughout Ohio (Urban 1978), but changes in land-use practices have led to range contraction and population declines throughout the state (Spinola and Gates 2008). We studied population ecology of bobwhites on private lands within the core of their current distribution in southwestern Ohio to understand the proximate factors contributing to ongoing population declines. Previous work found that non-breeding season survival in our population was low (5–12% during Oct–Mar; Janke and Gates 2012) and strongly influenced population growth rate (Gates et al. 2012). Winter weather appeared to be the primary influence on non-breeding season survival during our study, but additional factors such as habitat use and covey membership dynamics may also contribute to low survival (Janke 2011, Janke and Gates 2012). Here, we report covey movements and membership dynamics from our study using radiotelemetry and capture histories. We interpret our observations in light of previous studies from across the species' range. Because of the role that covey size plays in individual survival (Williams et al. 2003), we expected that bobwhites would move among coveys and that adjacent coveys would combine throughout the season as covey sizes declined because of high individual mortality.

METHODS

Study Area.—We studied bobwhite covey dynamics on four private land sites (400–1,200 ha) in Highland and Brown counties in southwestern Ohio (Fig. 1). Woodlots accounted for 8–29% of the sites and had primarily mature oak (*Quercus* spp.) and hickory (*Carya* spp.) overstories with sparse understories. Grasslands accounted for 9–20% of the sites. Row crop fields (predominately soybeans and corn) accounted for 38–72% of the sites. Landscape surrounding each site varied from low to high agriculture from south to north (17–62% of the area within 10 km of each site) and low to high forest cover from the northwest to southeast (21–50% of the area within 10 km buffer of each site). Temperatures recorded at a nearby weather station (NCDC 2011) during the study averaged 8.5 °C during both years and were colder than the 30-year average (10.5 °C). Snow accumulation during the first year of the study (101.6 cm) exceeded the 30-year average (67.5 cm), whereas snow accumulation in the second year was near average (67.3 cm). There were more days with ≥5 cm of snow cover than typical in the region in both years; 31 days in the first year of the study and

41 days in the second year of the study, compared with 19.8 days for the 30-year average.

Field Methods.—We searched each study site using covey call surveys (DeMaso et al. 1992) in the fall and systematic searches with pointing dogs and snow-tracking throughout the non-breeding season (Oct–Mar 2009–2011) to locate coveys. We limited the scope of our analyses to October–March to exclude early covey formation during September and covey break-up during April. We attempted to capture individuals in all coveys with baited funnel traps (Stoddard 1931) and targeted mist-netting (Wiley et al. 2012). We fit all individuals with a uniquely numbered aluminum leg band and recorded age, sex, and covey affiliation at the time of capture. A subset of individuals (>165 g body weight) in each covey were fitted with a 6.6 g necklace style radiotransmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA). Capture, handling, and marking protocols used in this study were reviewed and approved by the Animal Care and Use Committee at Ohio State University (protocol number 2007A0228).

We located each radiomarked individual once daily at least six times per week by homing and triangulation from short distances (≤20 m; White and Garrott 1990). We determined direction and approximate distance to the individual and recorded that location on a Global Positioning System (GPS; Garmin GPS Map 76, Garmin International Inc., Olathe, Kansas, USA) and recorded the habitat type in which the individual was located. Daily locations were distributed throughout the day to capture a full range of diurnal activity. We recorded whether all radio-marked individuals in the covey were together after locating each radiomarked bird. Individuals were recorded as separated if they were more than 30 m apart, which was approximately twice the telemetry location error in the study (Janke 2011) and therefore a distance at which investigators could effectively differentiate locations of radiomarked individuals. We attempted to maintain a sufficient distance from individuals to avoid regular flushing. We recorded the number of individuals in the covey when coveys were flushed incidentally.

Data Analysis.—We observed patterns of individual changes in covey affiliation or mergers of multiple coveys based on banding records, radiotelemetry locations, and field observations. We estimated annual covey densities on the sites as the number of coveys identified within the areas searched each year. We reported the frequency of radio-locations for which radiomarked birds in the same covey were separated by >30 m. We only used coveys with more than two individuals radiomarked for more than 30 days in our analyses. We tested for a weekly temporal trend in covey sizes throughout the season with a linear mixed-effects model in the *lme4* package in Program R (R Development Core Team 2012, version 2.15.1). Coveys were used as a random effect to account for repeated counts of the same covey through time. We specified a Poisson distribution with a log link because weekly covey counts were right-skewed. We tested models with only the random effect (i.e., no weekly variation in covey size), a weekly time trend through the season, a week plus year effect, and a week by year interaction and compared support for the four models based on differences in Akaike's Information Criteria (AIC) scores and weights (Akaike 1973, Burnham and Anderson 2002). We used the most parsimonious nested temporal model within 2 ΔAIC of the lowest AIC score (Arnold 2010) to predict the magnitude of weekly changes in covey flush counts.

We followed Guthery et al. (2005) to quantify usable space on each study site for each year as an indication of site-specific habitat availability (Wiley 2012). We classified radiolocations and tracts of contiguous cover types within the study areas into six categories (early succession herbaceous vegetation, early succession woody vegetation, forest, pasture, row crop, and other) and calculated selection ratios based on proportional use and availability (Manly et al. 2002). We used the area of the most selected cover type to calculate total area of usable space on each site (Guthery et al. 2005) and then reported percent usable space by dividing by the area of usable space by site area. We characterized movements of radiomarked coveys by calculating the Euclidean distance between telemetry locations where all individuals in the covey were together (hereafter covey points; Lohr et al. 2011). We divided the distance between the two locations by the elapsed time between locations and rescaled the movement estimate to minimum daily movement rates (MDM). We excluded locations not taken on successive days and only included coveys with ≥30 covey locations in the analysis. We measured the Euclidian distance from the centroid of each covey's locations to the nearest adjacent covey centroid as a metric to compare proximity among coveys at each site.

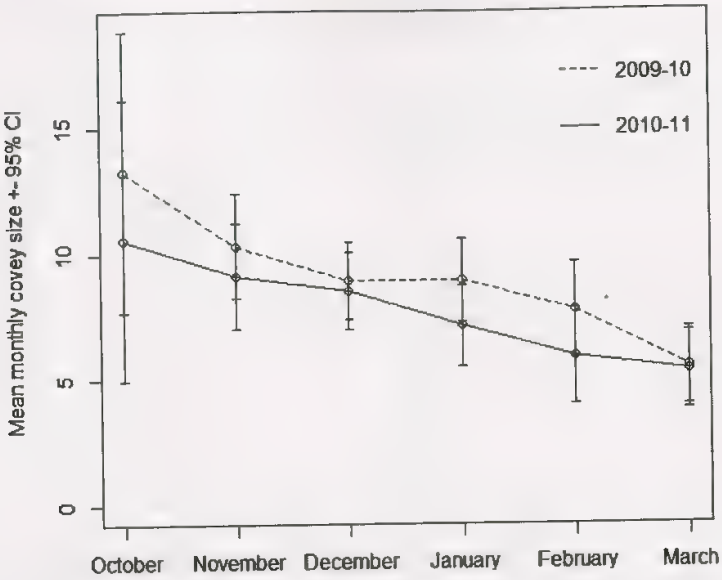

FIG. 2. Mean monthly covey sizes estimated based on covey flushes recorded on radiomarked coveys of Northern Bobwhites in southwestern Ohio during October–March 2009–2011.

We tested differences in MDM rates among months and study sites with analysis of variance (ANOVA) and among years with a *t*-test in Program R. We tested differences among covey distances by site with ANOVA and among years with a *t*-test in Program R. One covey was excluded from the analysis because it was the only covey present on the Peach site during the second year of the study. We also tested associations among inter-covey distances, covey densities, MDM, and usable space estimates ($n = 8$ site by year estimates) and reported results with $r > 0.5$.

RESULTS

We captured and leg-banded 413 unique individuals from 57 coveys during 2009–2010 ($n = 211$) and 2010–2011 ($n = 202$). Mean covey size in October was 11.9 individuals (range = 5.0–23.0 individuals) and declined throughout the season to a mean March covey size of 5.4 individuals (range = 1.0–9.5 individuals; Fig. 2). There was strong support for models with weekly trends in covey size (total $w_i = 1.0$) over the null model with no time variation ($\Delta AIC = 202.4$, $w_i = 0.00$), but no additional support for models with differences in annual intercepts or slopes ($\Delta AIC < 2$). Weekly predictions from the regression equation indicated that covey size declined an average of 3.2% (SD = 0.14) per week.

We recaptured 142 banded individuals and documented no cases where individuals changed covey affiliation. We radiomarked 307 individuals (mean 4.6 individuals/covey, SD = 2.3) and recorded one instance where a radio-marked individual changed covey affiliation. That individual returned to its previous covey after 14 days. One radiomarked bobwhite that was thought to be the only remaining individual in its covey joined a nearby covey on one occasion on the Wildcat site (22 Feb 2010). We documented six instances where two formerly distinct radiomarked coveys combined to form a single, larger covey (Table 1). Three mergers occurred during October and November (19 Nov 2009 on Wildcat, 27 Oct 2010 on Wildcat, and 9 Nov 2010 on Fee) and three covey mergers occurred during winter (14 Feb 2010 on Wildcat, 2 Jan 2011 on Fee, and 8 Jan 2011 on Wildcat). Two additional unconfirmed mergers were suspected for two coveys during March; one merger on the Thurner site was not complete by the end of the study on 31 March 2011, and one merger could not be confirmed because no individuals were radiomarked in the second covey near the edge of the Fee site at the end of the season in 2010.

Proportions of usable space varied among study sites from 5.5–21.3% (Table 1). Covey densities ranged from 0.25–1.63 coveys/km^2 (Table 1). Mean distance from the centroid of each covey

TABLE 1. Annual site summaries for proportion of usable space, Northern Bobwhite covey densities, distance to nearest neighboring coveys, frequencies of covey mergers, and mean movement rates from four private land study sites in southwestern Ohio studied during October–March 2009–2011.

Site	Year	Usable space (%)	*n*	Coveys/km^2	Min. distance[a]	Covey combinations[b]	Mean MDM[c]
Fee	2009–2010	6.6	7	0.63	0.88	0	138 (123)
	2010–2011	7.9	6	0.54	1.39	2	129 (121)
Wildcat	2009–2010	7.7	11	1.63	0.51	2	143 (131)
	2010–2011	7.8	12	1.31	0.56	2	145 (132)
Thurner	2009–2010	21.3	3	0.51	1.14	0	152 (129)
	2010–2011	16.3	6	0.94	0.73	0	152 (118)
Peach	2009–2010	5.5	2	0.65	1.16	0	67 (72)
	2010–2011	9.2	1	0.25	–	0	109 (78)

[a] Mean minimum distance between centroids of covey locations on each site (km)
[b] Number of occasions where two unique coveys combined to form a larger covey
[c] Mean minimum daily movement rate (m/day [SD])

to the centroid of the nearest covey was 787 ± 64 m and differed among sites ($F_{3, 43} = 8.0$, $P < 0.001$) but not years ($t = -0.402$, $P = 0.69$; Table 1). Mean MDM rate was 139 ± 2 m ($n = 48$ coveys). The distribution of MDM rates was right skewed and the median MDM was 105 m. We square root transformed MDM rates and found rates differed among months ($F_{5, 3749} = 36.62$, $P < 0.001$) and study sites ($F_{3, 3751} = 16.81$, $P < 0.001$) but not years ($t = -1.196$, $P = 0.23$). Daily movement rates were greatest during fall (Oct = 214.0 m/day, Nov = 191.2 m/day), decreased during winter (Dec = 145.9 m/day, Jan = 119.1 m/day, Feb = 125.1 m/day) and increased slightly before spring (Mar = 132.4 m/day). Mean annual MDM was positively correlated with proportion of usable space on our study sites (Fig. 3a; $r = 0.54$, $P = 0.168$). Mean distances between coveys was negatively correlated with covey density (Fig. 3b; $r = -0.88$, $P = 0.008$). All other correlations were <0.5.

DISCUSSION

We observed strong fidelity to coveys by individuals and only one occasion of a radio-marked or banded individual switching coveys. Additionally, covey affiliation and composition during our study was generally stable despite declining covey sizes through the non-breeding season. These results differ from observations in southern populations (e.g., Rosene 1969, Yoho and Dimmick 1972a, Lehmann 1984), but are interestingly consistent with a few observations from other northern populations (e.g., Murphy and Baskett 1952, Robel and Kemp 1997; but see Williams et al. 2004). This regional variation is not consistent with our prediction that covey membership would be more dynamic in northern populations where maintenance of optimal group sizes should be an adaptive response to low non-breeding season survival that characterizes these populations (Williams et al. 2003). The failure of bobwhites in our study area to maintain optimal covey sizes may have contributed to low survival rates in this population (Janke and Gates 2012) and has implications for conservation strategies for bobwhites in low-density and declining populations in northern regions of their range.

Differences in site attributes across the bobwhite range, such as habitat connectivity or covey densities, likely play a role in observed patterns of covey membership dynamics (Ellis et al. 1969, Rosene 1969, Yoho and Dimmick 1972a). Higher rates of individual movements among coveys are more likely when covey ranges overlap (Rosene 1969), and ranges are more likely to overlap in high-density populations or on sites with more continuous habitat (e.g., rangelands, forests; Ellis et al. 1969). Our estimates of covey density were considerably lower than previous estimates from populations in Texas (4–58 coveys/km^2, DeMaso et al. 1992; 4.1–6.2 coveys/km^2, Leif and Smith 1993), and generally lower than estimates from Illinois (2.4 coveys/km^2, Roseberry and Klimstra 1984), Kansas (1.2 coveys/km^2, Williams et al. 2004), and range-wide (3.1–4.7 coveys/km^2, Evans et al. 2013). Variation in covey densities among our sites also appeared to influence the proclivity for coveys to merge. Two of three confirmed winter covey mergers occurred on the site with the highest covey densities and lowest mean distance between covey location centroids. The other documented winter merger and the two suspected mergers occurred in the few areas

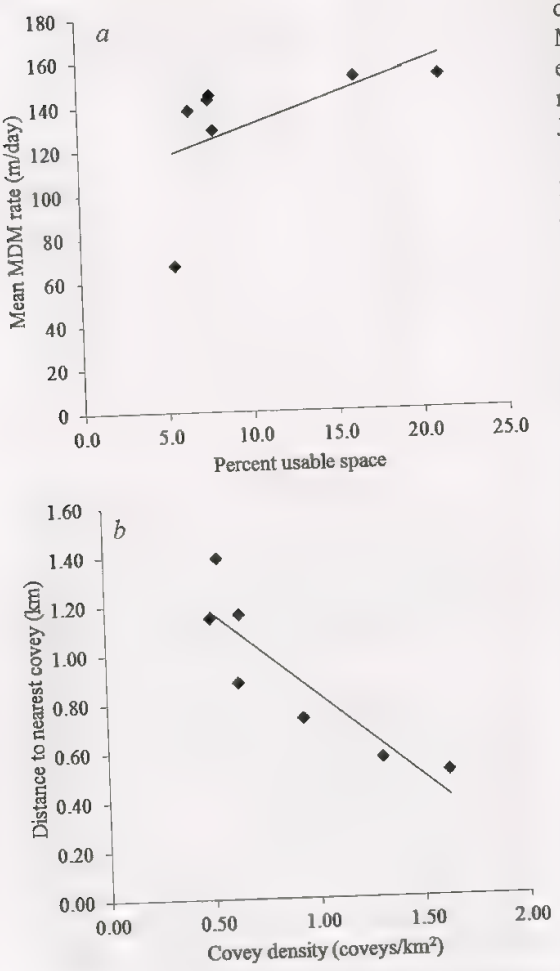

FIG 3. Relationship between site-specific usable space estimates and mean minimum daily movement (MDM) rates (a) and covey densities and distances to adjacent coveys (b) observed on four study areas in southwestern Ohio during October–March 2009–2010 and 2010–2011.

where covey ranges overlapped on the lower density study sites. The confirmed late-winter merger on the Fee site and the suspected March merger on the same site occurred in the same location in 2 consecutive years. Most other coveys were spatially isolated from other coveys throughout the non-breeding season. Continued radio-tracking of coveys on our study sites during 2012–2013 revealed a consistently low frequency of covey mergers ($n = 3$ mergers out of 20 coveys) despite declining covey sizes through the season (RJG, unpubl. data).

Increased movement rates could potentially compensate for low densities if individuals move more to interact with neighboring coveys in low density populations. However, our estimate of MDM rate (139 m/day) was among the lowest estimates for covey movements estimated from radiotelemetry studies in the literature (New Jersey: 160 m/day, Lohr et al. 2011; Kansas: 195–227 m/day, Madison et al. 2000; and 228–275 m/day, Williams et al. 2000; Tennessee: 431 m/day, Yoho and Dimmick 1972b). Additionally, our median MDM rate revealed 50% of daily movements recorded in our study were ≤105 m/day, considerably lower than previously reported. Although Williams et al. (2000) showed that low movement rates improved individual survival in their population, we contend that low movement rates diminish opportunities for interactions between coveys and may therefore negatively influence individual survival in low density populations.

Previous studies suggested that covey movement rates (Lohr et al. 2011) and density (Ellis et al. 1969, Exum et al. 1982) increase in landscapes with more suitable habitat (i.e., more usable space, *sensu* Guthery 1997). Two observations from our study lend support to the hypothesis that movement rates were driven by site-specific habitat characteristics. First, mean movement rates on our study areas were remarkably similar within sites during our study but were quite variable among sites. There was also a positive relationship between percent usable space and MDM rates on our study sites, suggesting bobwhites on sites with more suitable habitat moved more. Weather was likely also an important determinant of low observed movement rates (see Roseberry 1964). Even if our estimates of MDM rates were biased low because of severe winter weather, the implications of low movement rates are the same. Severe winter weather may influence survival through both a direct influence on individual survival (increased predation or exposure during snow events) and indirectly by inhibiting movements of coveys to combine and maintain group sizes to improve individual survival (Williams et al. 2003).

The patterns of covey membership and size dynamics observed during our study suggest that coveys in our low density population apparently failed to maintain optimal group size because of low contact rates with adjacent coveys. If maintaining optimal group size confers a survival advantage (as shown by Williams et al. 2003) and density influences the ability of coveys to interact as we have predicted, failure to maintain group

size in low density populations potentially represents an important Allee effect on non-breeding season survival. If density or habitat connectivity plays an important role in covey dynamics as we have argued, coveys in low density populations will be less able to maintain optimal group sizes, further depressing population growth rates (Sandercock et al. 2008, Gates et al. 2012) and reducing the ability of populations to withstand high non-breeding season mortality (Guthery et al. 2000). Additional research from study areas with varying densities, covey sizes, and habitat configurations is necessary to elucidate the specific influence of density on bobwhite covey dynamics and the role it may play in population dynamics. If covey membership dynamics are density dependent, management strategies should focus on increasing local densities of bobwhites rather than using widely dispersed habitat restoration or translocation programs that create widespread, low density populations that afford little opportunity for interaction among coveys.

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First Nesting Information on the Enigmatic Black Bushbird (*Neoctantes niger*)

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ABSTRACT.—We present the first nesting information for the Black Bushbird (*Neoctantes niger*), an enigmatic and poorly known member of the family Thamnophilidae. A hanging bulky cup nest was found in September 2011, in the buffer zone of Manu National Park, Peru. The nest contained a single white egg with scattered dark maroon spots and light streaks and was being attended by a male. The general shape of the nest resembled the deep pouch-shaped nests of other ant-

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birds (e.g., *Hypocnemis*, *Myrmotherula*) but with clear differences in overall dimensions, thickness and amount of nesting material. More information is needed on nest architecture and breeding behavior for the Black Bushbird and all of its possible close relatives. *Received 24 April 2013. Accepted 23 August 2013.*

Key words: Black Bushbird, egg, *Neoctantes niger*, nest, nesting biology, tropical.

The Black Bushbird (*Neoctantes niger*) is an enigmatic and poorly known member of the antbird family (Thamnophilidae). One of its most distinctive morphological traits is the bill shape with an upturned lower mandible, an unusual characteristic in the family that is also found only in two other species in the genus *Clytoctantes*. These two genera are known as the Bushbird group (Lanyon et al. 1990, Zimmer and Isler 2003, Whitney 2005). The current taxonomic classification treats the genus *Neoctantes* as monotypic (Remsen et al. 2013), and recent phylogenetic hypotheses suggest a close relationship between *Neoctantes* and antwrens in the genus *Epinecrophylla* (Irestedt et al. 2004, Brumfield et al. 2007, Gómez et al. 2010, Belmonte-Lopes et al. 2012, Bravo et al. 2012).

The Black Bushbird is rare to locally uncommon throughout its range; it is distributed mainly throughout northwestern Amazonia (south-central Colombia, eastern Ecuador, northeastern Peru and west Amazonian Brazil) with two isolated populations in southeastern Peru and eastern Amazonian Brazil (Ridgely and Tudor 1994, Zimmer and Isler 2003, Schulenberg et al. 2007). The secretive and skulking behavior of Black Bushbirds, coupled with their preference for areas of dense tangled growth around treefalls, light-gaps, and swampy forest streams, make it challenging to observe them (Zimmer and Isler 2003). All aspects of the natural history of Black Bushbirds are poorly known, and nothing has been published with regard to their breeding behavior (Zimmer and Isler 2003). Here, we provide the first nesting observations of Black Bushbirds based on an active nest found in the buffer zone of Manu National Park at Pantiacolla Lodge, Madre de Dios, Peru.

OBSERVATIONS

A nest of the Black Bushbird was found in the Pantiacolla Station, Madre de Dios, Peru (12° 38′ 31.3″ S, 71° 14′ 21.2″ W; 412 m elevation). The station is part of the Pantiacolla Lodge, which is located in the Amazonian lowland rainforest in the buffer zone of Manu National Park, a well-known destination for birding with about 500 species recorded (Walker 2009). We traversed the trail system in the area to search for nests of Black Bushbirds. The locale is comprised mainly of floodplain, terra firme habitats, and bamboo patches (*Guadua* spp.). Elevations of the study site range from 400–900 m. Monthly average temperature is 23.1 ± 2.5 °C (min-max = 13.6 to 39.1 °C) with a rainy season from November through April and a dry season from May through August.

On 27 September 2011 during a daily routine of nest searching, SD flushed a male Black Bushbird and discovered a cup nest with one egg (Figs. 1A-1B). We measured the nest and egg to the nearest 0.1 mm with calipers and weighed the egg and dry nest materials using a FlipScale F2 (My Weigh, Phoenix, Arizona, USA) digital pocket scale with an accuracy of ±0.05 g. A digital video camera was set 3 m from the nest and camouflaged with natural vegetation from 0845–1040 Peru Time (PET) to confirm the species. The nest was located 1 m above ground in a dense understory area with abundant stems and vine tangles and moderately open canopy (50%) in terra firme forest. The bulky cup nest was hanging from a horizontal fork of a 1.5-m small plant. The measurements (mm) of the nest were: inner diameters of the cup 82 × 77.1; outer diameters 122.6 × 124.5; wall thickness 35.3; cup depth 74.5; and overall height 140.2. The nest had three distinctive layers that weighed a total of 38.9 g; the external layer weighed 17.8 g and was made of dry tree leaves or fragments (20%), dry palm leaves (10%), and dry palm fibers (20%); these three materials were woven with dark brown rootlets of variable thickness (50%). The intermediate layer weighed 19.0 g and was a compact layer composed entirely of dry light-colored palm-like leaves. The most internal layer (cup lining) was composed of dry grass fibers (50%) and dark rootlets (50%) that weighed 1.0 g. A conspicuous amount of extra material hung asymmetrically from the outer wall and rim of the nest, and was maximally 250 mm in length (Fig. 1A).

One single egg was in the nest being incubated by the male. The egg was white with scattered dark maroon spots and light streaks mainly at the large end (Fig. 1C). It measured 23.6 × 16.8 mm and weighed 3.5 g. We recorded two incubation

FIG. 1. Nest, egg, and adult of Black Bushbird (*Neoctantes niger*) in Madre de Dios, Peru. (A) Lateral view of the bulky open cup suspended from a horizontal fork. (B) Nest with egg seen from above. (C) Lateral view of the egg. (D) Male adult in the rim of the nest.

events with the digital video camera that lasted 50 and 39 mins, respectively, and a foraging trip of 23 mins; the male approached and landed on the nest rim quietly (no vocalizations could be heard on the camera), turned once on the rim, and made a conspicuous upward and downward tail motion before hopping into the nest and starting incubation (Fig. 1D). A video of the nest is available at www.zoology.ubc.ca/~jankowsk/Manu_Videos.html. The nest was found empty the next day at 0730; the structure was moderately twisted to one side and eggshell fragments were found on the ground. We could not determine if predation or natural damage by heavy rain in the previous night were the cause of the failure.

DISCUSSION

The nest described here represents the first breeding information for the Black Bushbird. Recent molecular data suggest that *Neoctantes* is closely related to the "Checker-throated" group of antwrens, *Epinecrophylla* (Irestedt et al. 2004, Brumfield et al. 2007, Gómez et al. 2010, Belmonte-Lopes et al. 2012, Bravo et al. 2012).

However, none of these molecular analyses included the two species in the genus *Clytoctantes*, Rondonia Bushbird (*C. atrogularis*) and Recurve-billed Bushbird (*C. alixii*), that are suggested to be closely related to the Black Bushbird based on morphological, vocal, and behavioral similarities (Lanyon et al. 1990, Whitney 2005). However, Black Bushbirds have similar vocalizations to Rondonia Bushbirds (Whitney 2005) but differ from Recurve-billed Bushbirds, which suggest that the latter might not be as closely related to the other species as previously proposed (Laverde-R and Stiles 2007).

The nest architecture of Black Bushbirds is quite different from the supposed oven-shaped nest architecture with side entrances constructed by *Epinecrophylla* antwrens (Isler et al. 2006). However, Skutch (1969) described the nest of the Checker-throated Antwren (*Epinecrophylla fulviventris*) as a deep pensile pouch attached to a fork rather than as an oven-shaped nest, and this description resembles the general shape of a nest of a Black Bushbird. Unfortunately there are no nest descriptions for the Rondonia Bushbird or the Recurve-billed Bushbird, and thus it is impossible to make comparisons among these and the nest of the Black Bushbird.

The general shape of the Black Bushbird's nest, a bulky open cup suspended from a horizontal fork, resembles the deep pouch-shaped nests constructed with dry leaves and dark rootlets of other antbirds. These include Yellow-breasted Warbling-Antbird (*Hypocnemis subflava*: David and Londoño 2013), Amazonian Streaked-Antwren (*Myrmotherula multostriata*: Cadena et al. 2000) and Checker-throated Antwren (Skutch 1969). However, the Black Bushbird's nest was larger in all dimensions, thickness, material compactness, and amount of extra material pending from the nest, compared to the nests of these species. These differences could be related to the differences in body size between these species.

Two eggs comprise the typical clutch size of antbirds (Zimmer and Isler 2003), but incubation of one egg in the nest reported here suggests that this could be the clutch size of Black Bushbirds; however, it is also possible that one egg was already depredated on the nest. Incubation by the male during the day is also widely reported for antbird species (Zimmer and Isler 2003). Detailed information on nest architecture and breeding behavior for almost all species possibly related to the Black Bushbird is lacking and may be useful for understanding the evolutionary history and relationships of this enigmatic species.

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First Breeding Record of the White Tern, *Gygis alba*, in México

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ABSTRACT.—We report the first breeding record of the White Tern (*Gygis alba*) in México. We also provide notes on parental behavior of this species on Socorro Island, Revillagigedo Archipelago, México. We observed two adults feeding one nestling during the summer of 2012 at a nest located on the naval base on Socorro Island. The White Tern is considered a vagrant species in the Revillagigedo Archipelago. Although a breeding colony was mistakenly reported earlier, our report positively confirms for the first time the breeding status of this species in México. *Received 8 May 2013. Accepted 23 August 2013.*

Key words: breeding range, *Gygis alba*, Revillagigedo Archipelago, Socorro Island, White Tern.

The White Tern (*Gygis alba*) is widely distributed across tropical oceans (Harrison 1983). The majority of breeding colonies in the Pacific Ocean are found to the west, on Norfolk, Kermadec, Laysan, Marquesas, Hawaii and other South Pacific islands (e.g., Harrison 1983, Niethammer and Patrick 1998, Vanderwerf 2003). In the eastern Pacific Ocean, there are breeding colonies reported on Malpelo (Pitman et al. 1995) and Sala y Gómez (Vilina and Gazitua 1999) islands. In Central America, the known breeding range for the species is limited to Clipperton and Cocos islands. Clipperton is the closest breeding colony to Socorro Island (945 km); White Terns are potential casual visitors to coastal areas along tropical Central America and South America (Gifford 1913, Stager 1964, AOU 1998, Niethammer and Patrick 1998).

The species is considered vagrant on Socorro Island, México (Howell and Webb 1995). Gifford (1913) observed and collected one adult male at Roca O'Neil, México on 27 July 1905; the individual had fresh plumage indicating that molt was coming to an end. Based on this record, Friedmann et al. (1950) conjectured that a breeding colony was present at Roca O'Neil. Subsequent observers failed to find a breeding colony, and there were no further reports of the species in that area (Brattstrom and Howell 1956, Jehl and Parkes 1982, Howell and Webb 1990, Santaella and Sada 1991, Wehtje et al. 1993).

The breeding biology of the species is well documented. Breeding pairs lay one egg and in cases where two eggs have been recorded, often one of them is addled (Stager 1964). Eggs are laid directly on rock or tree ledges and there is no evidence of nest construction (Marshall 1949). On average, incubation takes about 36 days, fledgling about 43 days, post-fledgling about 70 days; the overall breeding effort is around 5 months

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FIG. 1. White Tern (*Gygis alba*) at the naval base on Socorro Island, Revillagigedo Archipelago, México. (A) White Tern nestling on a wall at the naval base. (B) White Tern adult carrying small fish in its beak. (Photographs by JEMG).

(Ashmole 1968, Marks and Hendricks 1989, Niethammer et al. 1992, Vanderwerf 2003).

On 10 August 2012, we observed a White Tern flying above the naval base on Socorro Island and found a chick sitting on the concrete wall of a building on 14 August 2012 (Fig. 1A); the adult scolded us as we approached the chick. During 15–17 August, the chick moved along the wall during the day to avoid sun exposure. On 18–19 August 2012, both adults perched near the chick during the day on the piping of a water vat. In the evening, the two adults arrived at the naval base and perched on the flag mast to spend the night; they brought small fish in their beaks but did not deliver any food to their chick those nights (Fig. 1B). On 20 August 2012, both adults fed the chick during the morning. We left the island that afternoon and were not able to continue our observations. We later received comments from naval personnel indicating that the birds were seen until December 2012. This indicates that the chick was about 15–25 days old when we made our observations, and the egg was probably laid in late June. Our observations confirm the breeding status of the White Tern in México on the same island where the species was first collected in México (Gifford 1913). This constitutes the first verifiable record of breeding White Terns on Socorro Island.

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An Unusual Foraging Tactic of the Willie Wagtail

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ABSTRACT.—We describe an undocumented foraging strategy of the Willie Wagtail (*Rhipidura leucophrys*) interacting with grazing animals. This observation includes intentionally displacing a horse in order to depredate insects. Further observations of the feeding behavior and foraging tactics of wagtails are necessary to ascertain the frequency of this event in this species that has adjusted to living in cities and rural settings. *Received 8 April 2013. Accepted 28 June 2013.*

Key words: Australia, feeding innovation, foraging behavior, natural history, urbanization.

The Willie Wagtail (*Rhipidura leucophrys*, hereafter wagtail) occurs on the Australian mainland, New Guinea, Solomon Islands, Bismarck Archipelago and Moluccas (Boles 1998). Wagtails are found in most open habitats, especially open forests and woodlands, and are common around human habitation (Higgins et al. 2006).

Although active in defending their territory, wagtails tolerate human infrastructure and activities associated with urban and rural settlements (Higgins et al. 2006). For example, they often feed and nest in close proximity to houses, and forage close to humans or domestic animals (Higgins et al. 2006). However, the mechanisms of their toleration of degraded and disturbed areas have not been determined.

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Diet and foraging behavior of the species have been studied in detail (Cameron 1985, Barker and Vestjens 1990, Adriano and Calver 1995, Dyrcz and Flinks 1995, Maxwell and Calver 1998, Webb-Pullman and Elgar 1998). Wagtails mainly feed on insects that are taken aerially or gleaned off the ground, foliage, branches, or tree trunks (Cameron 1985). Aerial prey is captured from a perch point, but terrestrial insects are flushed by sideways tail movements (Jackson and Elgar 1993, Higgins et al. 2006). They have also been reported to feed in association with mammals, including humans (Higgins et al. 2006).

Wagtails often forage in close proximity to both wild and domesticated animals in pastures and grasslands (Higgins et al. 2006). They either run behind or next to the moving animal to capture insects as they are displaced or sally from the animal's back. Here, we describe a previously undocumented wagtail feeding behavior which occurs while interacting with domestic grazing animals.

OBSERVATIONS

The observation took place at University of Wollongong, New South Wales, Australia (34° 24′ 17″ S, 150° 52′ 15″ E) where there was an open grassland with approximately six horses (*Equus caballus*) grazing daily.

On 24 April 2012 at 1010 AEST (Australian Eastern Standard Time), we observed two wagtails following a horse for ~80 secs. During the first 30 secs, the birds darted back and forth off the horse's back, sallying occasionally to the

ground. The birds mostly depredated flying insects while the horse grazed slowly. During the next 15 secs, the horse stopped grazing, and the birds ceased capturing insects. Suddenly, one of the birds made three quick and unexpected swoops onto the horse's ear, provoking it to shake its head. After shaking its head quickly, the horse walked because of persistence from the bird. Once the horse began to walk, the bird stopped disturbing it and both birds flew to the ground. They walked in front of its head for the next 20 secs and made several brief attempts to capture insects. The horse again ceased grazing activity for 10 secs, during which one of the birds returned to the horse's back and the other flew away.

During 5 secs when one bird gently gleaned insects off the horse's back, the horse did not show any sign of irritation. Suddenly, the bird quickly climbed up the horse's neck and swooped at its ear again. The horse's movement was apparently provoked by the bird, and as soon as the horse moved, the bird returned to the grass to capture insects while running short sprints next to the horse.

On 1 June 2012 from 0930 to 0940 hrs, we observed a wagtail riding on the back of a grazing horse. The bird sallied and gleaned insects from the horse's back without the horse exhibiting any irritation. During the following 10 mins, we recorded five similar observations of the bird irritating the horse when it ceased moving and grazing. The wagtail succeeded in forcing the horse to move on all occasions. The bird was consistently seen capturing insects close to the horse each time after antagonizing the horse.

DISCUSSION

Foraging associations between birds and other animals have been widely reported in the literature. Most cases of such interactions occur between mammals and birds, particularly ungulates and passerines (Tomazzoni et al. 2005), where the back of the host is used as a perch (for sallying) or beating (for feeding on insects disturbed during grazing). Although there is substantial knowledge of wagtail foraging behavior as it relates to interactions with domestic and wild animals (Higgins et al. 2006), we found no mention of wagtails (or any other passerine) feeding in the manner we describe (Lefebvre et al. 1997, 1998, 2002; Nicolakakis and Lefebvre 2000; Higgins et al. 2006). However, Cattle Egrets (*Bubulcus ibis*) have been known to influence vertebrates in a manner that increases the potential of the egrets to capture insects (Dawn 1959, John and Lee 2012).

Although our observations were limited, we interpret the birds' swooping behaviors as intended to make the horse move to flush insects. We suggest this based on: (1) the bird only swooped when the horses did not graze or walk; (2) bird instigation ceased when the horse returned to walking; (3) the bird actively returned to capturing insects once the horse grazed again; and (4) the behavior did not occur while the horse was actively grazing. Additionally, the horse ignored the presence and movements of the birds on its back, but immediately responded with irritation when the bird flew at its ears.

Although wagtails glean ticks from the skin of grazing animals (Barker and Vestjens 1990, Higgins et al. 2006), and we observed them gleaning a horse's back, the functional purpose of flying at the ears was not to glean ectoparasites. Wagtails typically approach gently when taking insects from an animal's skin. However, when they approached the ears the birds moved quickly followed by sustained flight, similar to harassing when protecting territories (Boles 1988) only shorter in duration and without audible sound.

Wagtails are highly aggressive and fearless when defending their territory during the breeding season (Boles 1988, Dyrcz 1994, Dyrcz and Flinks 1995). However, our observations did not involve territorial defense, because they took place outside the breeding season.

Mechanisms permitting some species (e.g., wagtails in urban and agrarian areas) thriving and tolerating fragmented and disturbed habitats have not been established. Among the cited traits that might permit a bird to adjust and succeed in novel environments (such as urbanized areas) are the behavioral flexibility and feeding innovations (Lefebvre et al. 1997, 1998; Nicolakakis and Lefebvre 2000) which could be defined as foraging behaviors, ingesting a new type of food, or using a new foraging technique observed or reported for the first time (Lefebvre et al. 1997, Delgado-V. and Brooks 2003, Kark et al. 2007). Further observations of foraging strategies of wagtails would help determine if unusual facets, such as that described here, are changes and innovative patterns acquired by certain populations or just an individually isolated behavior.

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Yuba Mundo bicycle which was donated to CADV by CargoCycles (Australia), and Yuba Bicycles (USA) for conducting urban ecology studies. CADV received a PhD scholarship from University of Wollongong.

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Prevalence of Bird Blow Fly Infestation in Nests of the European Blackbird (*Turdus merula*)

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ABSTRACT.—Larvae of bird blow flies are hematophagous intermittent parasites and they infect a variety of bird host species. In this study we focused on the prevalence of infestation in nests of *Turdus merula* in two sites with different climate. We collected 57 nests from Bratislava (Slovakia) which has a warmer climate and 37 nests from Leipzig (Germany) where there is cooler weather during the breeding season. There is no significant difference in the prevalence of infestation and in number of puparia between these two sites. The average number of infested nests was 18.68% while the average number of blow flies per nest was

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10.0 ± 7.32 with 2.54 ± 1.83 larvae per nestling.

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Key words: bird blow fly, prevalence of infestation, *Protocalliphora* spp., *Turdus merula*.

The parasite-host interaction is probably the most common relationship between two animals and we find a variety of ectoparasites in bird nests. Larvae of bird blow flies are obligatory blood-feeding ectoparasites. They parasitize the nestlings of altricial bird species and can cause serious health problems (Sabrosky et al. 1989, Wesołowski 2001, Puchala 2004). The host range is wide, including mostly passerines (Gregor and Povolný 1959, Rognes 1991, Whitworth 2003, Jamriška et al. 2010). The prevalence of infestation by avian blow flies in birds' nests may be an important factor related to host population dynamics and structure (Hurtrez-Boussès et al. 1997, Puchala 2004). It is difficult to determine the total number and species of parasites in a nest; however, empty puparia are a reliable clue. The empty puparium is usually the only evidence of the presence of bird blow flies in bird nests once adult flies emerge shortly after nestlings fledge.

The Common Blackbird, *Turdus merula* Linnaeus 1758, is widespread throughout Europe (Ferianc 1979, Glutz von Blotzheim and Bauer 1988). These birds live in parks, woodland areas, cemeteries and gardens. Generally, their nests are cup-shaped and located in trees, bushes, or buildings. Nests are composed of twigs, sticks, grass, and leaves held together with mud. Nestlings fledge within 13–15 days (Ferianc 1979, Pikula and Beklová 1983), which is an important period for the development of blood feeding ectoparasites. In this study, we focused on the prevalence of infestation of blow flies in nests of *T. merula*, as one of the factors that can influence the breeding success.

METHODS

The present study was carried out during years 2007–2012 in two localities: Bratislava (48° 08′ 38″ N, 17° 06′ 35″ E, Slovakia) and Leipzig (51° 20′ 0″ N, 12° 23′ 0″ E, Germany). Studied areas were similar public parks with green bushes and trees, but with different climates. In Leipzig there is a cooler climate, while in the area around Bratislava the weather is warmer during the breeding season. All nests were gathered and transported in sealed plastic bags after nestlings fledged. Nests were carefully examined under laboratory conditions, and all stages of blow flies were recorded. The pre-imaginal stages were identified according to Cais et al. (2001), Draber-Moňko (2002) and Jánošková et al. (2010), adults were identified according to Rognes (1991). The prevalence of infestation was estimated only in nests with successful breeding where nestlings had fledged. The average number of larvae per nestling was estimated with respect to the number of hatched chicks in parasitized nests, not number of eggs. All statistical analyses were performed using the Program R (R Core Development Team 2012). For the comparison of prevalence of infestation between the two localities we used chi-squared test and the number of blow flies found per nest were compared with Student's *t*-test. Means are followed with standard deviation, minimum (min), maximum (max), and standard error (SE).

PREVALENCE AND ABUNDANCE OF INFESTATION

We collected 91 nests. These nests were from two central European localities: 57 nests from Bratislava, Slovakia, and 34 nests from Leipzig, Germany. On average, 18.68% of nests were infected, while the average number of blow flies per nest was 10.0 ± 7.32 (min = 1, max = 27, SE = 1.78) with 2.54 ± 1.83 (min = 0.33, max = 6.75, SE = 0.44) larvae per nestling. Almost all puparia specimens were identified as *Protocalliphora azurea* Fallen 1817. In one nest from Leipzig, there was mixed infestation with eight puparia of *P. azurea* and three puparia of *P. falcozi* Séguy 1928. Almost 18% of nests (Table 1) from Bratislava and 21% of nests from Leipzig were infected with blow flies. The average number of puparia found in nests of *T. merula* in Bratislava is 10.9 ± 7.95 (min = 2, max = 27, SE = 2.51) and in Leipzig 8.71 ± 6.7 (min = 1, max = 21, SE = 2.53). The average number of larvae per nestling in Bratislava is 2.83 ± 2.12 (min = 0.5, max = 6.75, SE = 0.67) and in Leipzig 2.14 ± 1.35 (min = 0.33, max = 4.2, SE = 0.51). In general, there was no significant difference in prevalence of infestation (X^2 = 0.007, P = 0.93) and in number of puparia (t =0.61, P = 0.55) between these two sites.

DISCUSSION

Factors affecting the presence and number of ectoparasitic blow flies in bird nests are poorly

TABLE 1. Number of infested nests with average number of blow flies.

Locality	No. of nests	No. of infected nests	Percentage (%)	Average No. of blow fly specimens
Bratislava (SVK)	57	10	17.54	10.9
Leipzig (GER)	34	7	20.59	8.71
Sum	91	17	18.68	10.0

understood and further studies are needed. Temperature, humidity, nest construction, or number of nestlings, are all important factors for ectoparasites. These larvae live among nest material and occasionally remain on nestlings (Sabrosky et al. 1989, Bennett and Whitworth 1991). Blackbird nests are usually robust, made of twigs, sticks, grass and leaves with muddy cup-shaped bottom and a lining of fine and soft grasses. Thus, blackbird nests represent a suitable environment for different groups of ectoparasites, such as mites, fleas, and blood sucking larvae or flies (Davis et al. 1971, Jamriška et al. 2011). We found an infestation rate of 18.68% with an average of 10.0 ± 7.32 larvae per nest. This represents 2.54 ± 1.83 larvae per nestling. The prevalence of infestation in non-cavity nesting birds is, for instance, in Savannah Sparrow (*Passerculus sandwichensis*) 17.9–63.3% with *Protocalliphora spatulata* (Sabrosky et al. 1989), and the average parasite load per nestling is 2.9 ± 0.29 (Fair and Miller 1995). The infestation rate by *Trypocalliphora braueri* Hendel 1901 in Meadow Pipit (*Anthus pratensis*) is just about 3%, and in the Bluethroat (*Luscinia svecica*), it is 4.2% with the average number 9.15 ± 0.75 of larvae per nestling (Pavel et al. 2008). On the contrary, more than 90% of nests of Blue Tits (*Cyanistes caeruleus*) are infested with blow flies, and the parasite infestation can reach up to 100 larvae per nest where the mean parasitic load is 13.53 ± 5.13 larvae per nestling (Hurtrez-Boussès et al. 1997). Gold and Dahlsten (1989) noted that *Protocalliphora* spp. (later identified by Sabrosky et al. [1989] as *P. parorum*; Sabrosky et al. 1989) infested 95.1% of Chestnut-backed Chickadees' (*Poecile rufescens*) and Mountain Chickadees' (*Poecile gambeli*) nests with mean number 37.2 ± 4.4 of larvae per nest. Eeva et al. (1994) recorded that 60% of nests of Great Tits (*Parus major*) and 32% of nests of European Pied Flycatchers (*Ficedula hypoleuca*) were parasitized by *P. azurea* larvae. The mean number of larvae per nestling was 2.0 ± 0.27 for *P. major* and 2.4 ± 0.36 for *F. hypoleuca*. In their study of several bird species, Bennett and Whitworth (1992) concluded, that in colonial and non-colonial cavity nesters with compact nests without feces, re-nesting in the same area resulted in high infestation rates. These nests are usually infested only by a single species of *Protocalliphora* spp. Many authors recorded low infestation rates or absence of blow flies in cavity nests of woodpeckers (Bennett and Whitworth 1992, Iwasa et al. 1995, Wiebe 2009). On the contrary, in some non-cavity nesters with large nests, such as crows, magpies and hawks, the infestation rate can be very high (Bennett and Whitworth 1992, Whitworth and Bennett 1992, Dykstra et al. 2012). Comparing our results with accessible records we conclude that the prevalence of infestation of blow flies in cavity nesters is, with some exceptions, higher than in non-cavity nesting hosts, and therefore, nest microclimatic factors together with host ecology, play an important role in the parasitism of blackbird nests.

Several studies demonstrate that bird blow flies can decrease growth and survival of nestlings and in cases of massive infestation, can cause anemia (Whitworth and Bennett 1992, Merino and Potti 1995, Hurtrez-Boussès et al. 1997, Puchala 2004). Despite the fact that larvae of *Protocalliphora* spp. reduce haemoglobin and haematocrit values of nestlings, seldom is their number in birds' nests so high that they cause death of nestlings (Whitworth and Bennett 1992). However, the impact of parasitism on nestling birds is complex, and we should evaluate all parasite species found in nests when considering the effect of parasites on nestlings in general. Knowledge about prevalence of infestation of blow flies in host species can help us to understand parasite dynamics and clarify what factors mainly affect nest infestation.

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William and Nancy Klamm Service Award for 2013: Clait E. Braun

The Wilson Ornithological Society established the William and Nancy Klamm Service Award in 2007 to honor the memory of Bill and Nancy Klamm, who generously supported the society with both their time and a substantial financial bequest. This award recognizes the reliance of a non-profit society on the generous donation of time and money of countless people who serve many roles within the Society including committee members, committee chairs, council members, officers, editors, article reviewers, editorial assistants, and local hosts. The Klamm Service Award recognizes someone who has an extensive history of service to the Society.

Clait Braun has been a long-time supporter of and advocate for the Wilson Society. Clait began his service to the Society as Chair of the Conservation Committee in 1975. In 1977, he was elected to the Wilson Council. He was elected Second Vice-President in 1981, First Vice-President in 1983, and President in 1985. Like many of the people who have been elected as an officer of the society, Clait served the Society in a variety of ways, having served on the membership committee, on the nominations committee, on the publications committee, on a local committee, and as chair of numerous scientific sessions. What is truly remarkable about Clait is his service after being an officer. He has served on the committees selecting student research awards, student presentation awards, and the best paper in the Society's journal. For the last 20 years, Clait has been a strong proponent for and an active participant in the Wilson Ornithological Society's journal. He served as the Chair of the Publications Committee, on the editorial board of the journal under three different editors, and, for the last six years, as the Editor of the *Wilson Journal of Ornithology*. He has encouraged authors to submit manuscripts, helped authors refine their submissions (especially international authors), and ensured the high standards of the journal. For his

almost four decades of service, and in anticipation of many more years to come, we award Clait E. Braun the 2013 Klamm Service Award with sincere admiration and gratitude.

To honor the recipient of the Klamm Service Award, the society commissions an original painting of a bird that is special to the recipient. The 2013 award is an original painting by Julie Zickefoose of Gunnison Sage-Grouse. Our choice of the lekking Gunnison Sage-Grouse not only reflects a species that is meaningful to Clait, but also a species that was first described in the *Wilson Bulletin* in 2000—one of three articles co-authored by Clait that have won the Edwards Prize for best paper in the Wilson journal.—Sara R. Morris (chair), Richard C. Banks, Charles R. Blem, Leann B. Blem, Jerome A. Jackson, and Doris J. Watt (Klamm Service Award Committee).

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Ornithological Literature

Margaret A. Voss, Book Review Editor

OWLS. By Marianne Taylor. Comstock Publishing Associates, Ithaca, New York, USA. 2012: 224 pages. ISBN: 978-0-8014-5181-2. $35.00 (hardcover).—Owls have intrigued humans throughout our history; we have placed their images on ancient coins and other artwork. Owls have been woven into our literary history, and even recently occupy prominent positions in the *Harry Potter* and *Guardians of Ga'Hoole* book series. Why are we fascinated with owls? Are the myths about owls true? This book provides the answers to these questions, and more. We reviewed this book as a team, a 15-year-old boy and his father, to provide contrasting perspectives on the book.

Tristan has gained interest in owls because he has not learned much about owls in school; the lack of information tends to create intrigue. Tristan started his search for information on owls at an early age, and he has even tried looking for some around our house and at campsites on vacations. Yet, he mostly has seen silhouettes and flourishes of wings. He likes to find books about owls to learn more facts that will help him understand them.

Larkin is a wildlife ecologist, but does not study owls. However, owls started him on his professional journey. As a member of the nature staff of the Iowa 4-H Camp in college, he learned to call Barred Owls (*Strix varia*), and it remains the only bird call that he can do well. Larkin gave lectures to campers in which he stuck his fingers in the skull of a study skin of a Great Horned Owl (*Bubo virginianus*) to show how they triangulate to find food in the dark. That fall, Larkin switched his career goal from veterinarian to research biologist.

Taylor's book is written in two sections: the first provides a description of owl characteristics, their habitats, life history, interactions with people, and conservation status; the second section is a compendium of 41 individual accounts of species found in North America and Eurasia. Throughout the book, Taylor has gathered photographs (a monumental effort) of owls from a host of photographers throughout the world. Tristan found the first section interesting because you learn about all of the characteristics of owls.

Tristan also found every single photograph in the book to be amazing, even though he has found almost any picture of owls to be amazing. Tristan suggested that the photos could have been overlaid with the species' common names to assist readers who open the book to a random page. Larkin agreed that the photographs were high-quality close-ups that show details of owl morphology, and the photos especially convey how owls blend with their environment. The photographs of owls in flight were especially good. The lone exception was the last species account of the Marsh Owl (*Asio capensis*). The photos were strikingly poor quality compared to all others, but Tristan guessed that this species may have fewer photos available. Regardless, the preponderance of photos is rich with detail and captivating.

We believe this book could be used by owl lovers in the general public, ornithologists, bird watchers, and students who need to find information for reports on owls. We found the book easy to access, and it was generally arranged in a good manner. Taylor provides an index, a very nice glossary of terms, and useful introductions to the book and to its two sections; all of these features serve to make the book accessible to a wide audience. Thus, the public should be able to understand the species accounts that are written at a higher level than the first section of the book. We believe that most readers will find their favorite owls included in the species accounts. Tristan was pleased to find all of his friends from *Guardians of Ga'Hoole* (Lasky, K., 2003).

The information provided by the book was useful. The species accounts provide information on range, evolution and relationships, a description, geographical variation, movements and migration, voice, habitat, behavior, hunting, diet, breeding, and conservation status. The IUCN status is used for the latter, and no details on conservation status are provided for sub-species. This broad approach glosses over some details. An example: Spotted Owls (*Strix occidentalis*) are listed as near-threatened by the IUCN, but the book does not mention that the Northern Spotted Owl (*Strix occidentalis caurina*) is listed as threatened in the United States.

The book is written in a style that was not too scientific to avoid stifling a reader's interest. Larkin thought the book could have been improved with a map of the range of each species, because the species accounts are not ordered geographically. Thus, there is no quick way to determine range without reading deep into the account. Tristan agreed that such maps would especially help younger students who are writing reports. We also thought that an icon or color-code might have been useful to indicate the species' conservation status to readers quickly.

Tristan regarded the font used in the book as adequate, but Larkin felt that a larger font with seraphs would have helped his middle-aged eyes. Tristan noted that one gets a sense that the book is primarily about the photographs, because the photos are so large and the text is so small. Some readers may only skim the rich photographs in the book, while other readers may read the text from cover to cover. But, the book's layout does not provide a middle ground; there are no icons, maps, text break-outs, and only one illustration. A reader who scans the photographs will not glean much information quickly. Although the sheer number of photographs is immense, the book could have been improved with some modern graphic design techniques to quickly draw a causal reader's eyes to more information.

Larkin was also confused by the order in which the species accounts were provided. We could find no explanations or apparent logical order in which the species appear in the second section of the book. The species accounts were not in the order of owls within the taxonomy overview that preceded the accounts, which made the second section difficult to use without returning to the table of contents in the front of the book.

The book has 26 sources cited, which suggests that this is a work for a popular audience. Taylor does not draw much information from primary literature for the species accounts, and relies on other reviews. Intriguingly, the Birds of North America (Poole, A., ed., 2005.) series was not among the sources used for the book.

We serendipitously found the book *Owls: their natural and unnatural history* (Sparks and Soper, 1970, Facts on File, New York, NY) in our Minnesota rental cabin as we completed this review. Sparks and Soper (1970) provided no species accounts, and instead elaborated on many of the topics covered in the first section of Taylor's book. Sparks and Soper (1970) made extensive use of line drawings to illustrate diet composition, owl population trends in relation to prey density, components of an owl pellet, sonographs of calls, and many morphological concepts. Taylor addresses many of these objectives with captivating photos. Both Tristan and Larkin thought Taylor's book might have benefited from illustrations that proved useful in the book by Sparks and Soper (1970). For example, an illustration of an owl skull and skeleton would complement Taylor's common reference to the fact that many owls appear much larger than their actual skeletal mass. The sole illustration in Taylor's book was of a "bird eye," and it was useful. But, Taylor failed to note that the drawing was specifically of a general avian species that hunts at night, such as most owls. Sparks and Soper (1970) provided cross-sections of both diurnal and nocturnal species to emphasize the specialization of owls' eyes.

Regardless of some shortcomings in layout design and content, Taylor's attractive book should make a nice addition to any book shelf or coffee table. It provides a wealth of information, especially for those in the general public who yearn to learn about owls. But, Taylor's book will most likely be remembered for the striking photographs that she has accumulated to bring reclusive owls into our homes.—TRISTAN R. POWELL, Lincoln High School, Lincoln, NE 68510, USA, and LARKIN A. POWELL, School of Natural Resources, University of Nebraska-Lincoln, Lincoln, NE 68583-0974, USA; e-mail: lpowell3@unl.edu

THE BOREAL OWL: ECOLOGY, BEHAVIOUR AND CONSERVATION OF A FOREST-DWELLING PREDATOR. By Erkki Korpimäki and Harri Hakkarainen. Cambridge University Press, Cambridge, UK. 2012: xiv + 359 pages, 32 color plates, numerous figures and tables. ISBN: 978-0-521-11371-7. $95.00 (hardcover).—Erkki Korpimäki first put up nest boxes in Finland in the fall of 1965 at age 13 and found his first nest of Boreal Owls (*Aegolius funereus*) the following spring. Forty-seven years, some 1,600 nests, and more than 100 publications later, he's still at it. I am fairly certain that no one has studied a single species of nocturnal raptor as thoroughly, or produced as many scholarly publications on that species, as Korpimäki. Here, Korpimäki and his former doctoral student Harri Hakkarainen have distilled decades of research into a package that

details the life history of this fascinating bird and its complex interactions with the three species of voles that make up the bulk of its diet and profoundly influence its behavior and demography.

The book is written for informed laypersons, graduate students, professional biologists, and anyone with an interest in owl ecology, predator-prey relations, and boreal ecosystems. It is organized into 15 chapters that cover basic biology, study area and methods, nesting and roosting habitat, foraging behavior and diet, morphological characteristics, sexual size dimorphism, mating systems and parental care, breeding biology and fecundity, movement patterns, survivorship and mortality, population regulation, and conservation. Throughout, Korpimäki and Hakkarainen present a sizeable amount of data, interpret their findings in the context of current theories of life-history evolution, and compare their data with information from numerous other published studies. The result is a superb autecological study and a great example of how life-history theory can be applied to a comprehensive, long-term data set derived from a large sample of marked individuals.

The study area covered 35 km^2 at the start and was expanded several times to its current size of 1,300 km^2 by 1988. Natural cavities were scarce, and most of the data were taken from owls that nested in boxes, which numbered 35 in 1966 and gradually increased to 500 by 1988. The number of nesting attempts ranged from two out of 61 boxes in 1968 to an incredible 163 out of 500 boxes in 1992. At the peak of box numbers, it took two people 7–10 days to check them all. Korpimäki and Hakkarainen and their colleagues made >41,000 box-visits from 1966–2009. At about 15 mins per visit, and converted to a 40-hr work week, this effort consumed nearly 5 years of field time! (In a humorous aside, Hakkarainen notes on page xiii of the Preface that boxes were checked more efficiently starting in 1992, when researchers abandoned climbing spurs in favor of "the ladder technique" introduced by another doctoral student.) The field effort paid off nicely, and through 2009 Korpimäki and Hakkarainen had banded the female at 1,224 nests, the male at 957 nests, and 4,158 nestlings, in addition to recapturing many breeding adults in subsequent years.

The study area is composed of 61% forest lands (65% pine, 30% spruce, 5% deciduous), 25% agricultural lands (including croplands and pastures), and smaller amounts of peat bogs, wetlands, and inhabited areas. Forests are heavily managed, and only 1% of the study area is in old growth. Owl diets are dominated by two species of *Microtus* voles and the bank vole, *Myodes* [*Clethrionomys*] *glareolus*. The two *Microtus* occur in agricultural fields and pastures. In contrast, the bank vole lives in forests and is three times more abundant in spruce than in pine. Relative to pine forest, spruce forest also has higher densities of alternative prey (small birds) and lower densities of nest predators. Accordingly, owls nest preferentially, and have the highest nesting success and productivity, in boxes placed in spruce forest close to agricultural lands.

More than 90% of owl nests are in boxes, with most of the remainder in cavities excavated by Europe's largest picid, the Black Woodpecker (*Dryocopus martius*). Owls prefer boxes over woodpecker cavities and lay significantly larger clutches in boxes (5.8 versus 4.96 in woodpecker cavities), probably because the floor area of boxes is larger than that of woodpecker cavities. In addition, woodpecker cavities have larger entrance holes, which probably make owl nests in natural cavities more vulnerable to predators like European pine martens (*Martes martes*) and larger owls. The occupancy rate of nest boxes declined with box age, perhaps because box quality declined with age, or predation risk increased with time owing to long-term memory of nest predators. Using a clever experiment with various combinations of new versus old boxes that were and were not relocated, Korpimäki and Hakkarainen found little support for the nest-quality and predation-risk hypotheses and suggest instead that their results are consistent with the food-depletion hypothesis in which breeding pairs reduce vole densities over time. They further posit that food depletion is more likely to explain nest shifts at high latitudes where vole populations are cyclic than farther south where environmental conditions and vole numbers are more stable from year to year.

By snap-trapping small mammals in the field and examining stored prey in boxes, Korpimäki and Hakkarainen determined that owls killed more male than female voles and preyed selectively on smaller, lighter individuals. They suggest that larger, dominant voles occupy habitats with denser vegetation that are safer from predators and force less-dominant individuals into areas with higher predation risk. The numerical response of Boreal Owls to peaks in the vole cycle included increases in male survival, nesting density, clutch size, fledgling production, and incidence of polygyny and polyandry. The functional response curve of

predation across a vole cycle was nearly linear, indicating that owls took a constant proportion of the available number of voles. This pattern also was exhibited by Eurasian Kestrels (*Falco tinnunculus*), Long-eared Owls (*Asio otus*), and Short-eared Owls (*Asio flammeus*) in the study area and lent support to the notion that at peak vole densities, many predators switch to eating voles, which induces high interference competition within and among predator species (which also include several other owls and mammals) such that no one species can subsist entirely on voles. With so many predators shifting to a vole diet during peaks in the cycle, do Boreal Owls and the other sympatric predators regulate vole populations? The pooled functional and numerical responses of kestrels, Boreal Owls, Long-eared Owls, and Short-eared Owls indicated that vole predation was positively density dependent and suggested that predation dampened vole populations by truncating numbers during peaks in the cycle.

Like many biologists who study raptors, Korpimäki and Hakkarainen were curious about so-called reversed size dimorphism wherein females are larger than males. They failed to find support for the main hypotheses that focus on increased female size (e.g., starvation, reproductive effort, female dominance, and sexual selection) but had support for the small-male hypothesis, which posits that small size confers advantages in foraging efficiency and perhaps territory defense. Once again, fluctuating food availability was important in that small males were better providers than large males in low vole years. During vole peaks, however, larger males were the best providers, indicating that no one phenotype is best across the range of food availability. Korpimäki and Hakkarainen reasonably conclude that reversed size dimorphism is unlikely to result from a single selective force.

Owing to a personal bias on the subject, I found the chapter on mating systems and parental care especially intriguing. Both pair members were captured at 923 nests, and in only three cases did a pair stay together for more than one breeding season. In two of these cases the birds nested two years in a row, and in one instance they had different mates the year after they first paired and then reunited in year three. In all three cases the birds used the same boxes for each attempt together, and Korpimäki and Hakkarainen suggest, with admittedly scanty data, "that it is probably the nest site rather than the mate that makes the pair bond of Boreal Owls last for more than one breeding season" (page 148). The primary reason that pair bonds dissolve so readily is that male Boreal Owls tend to occupy the same territory for life, whereas females are highly mobile, sometimes moving >500 km between successful breeding attempts. Korpimäki and Hakkarainen also examined whether Boreal Owls mate assortatively by age. Relative to chance expectations, during the increase phase of the vole cycle, 2-year-old males and older mated more often with the oldest (>2 yrs) females, whereas during the decline phase in the cycle, yearling and 2-year-old males paired more often with yearling females. Yearling males seldom bred during troughs in the vole cycle, so too few data were available to evaluate assortative mating during this period. The most likely mechanism for assortative mating by age is female choice based on food-provisioning rates of males.

Like the handful of owl species that have been studied elsewhere, Boreal Owls in Finland are genetically monogamous, no doubt because food provisioning by males is so essential to successful reproduction that females do not risk losing the cooperation of their mates by seeking extra-pair copulations. Seventy-two cases of polygyny were documented, including three males that cared for three broods simultaneously (i.e., trigyny). DNA fingerprinting confirmed that each polygynous male sired all of the young he provisioned. Not surprisingly, polygyny was positively correlated with vole abundance and was never recorded during lows in the vole cycle. Primary and secondary nests of polygynous males averaged 1,350 m apart, the distance often encompassing several suitable nest cavities or unoccupied boxes. Primary and secondary females laid similar clutch sizes, but primary females fledged more and heavier young than did secondary females. Because primary and secondary females had similar amounts of stored prey during laying and incubation and laid the same number of eggs, Korpimäki and Hakkarainen conclude that polygynous males fed their second females at the expense of their first females early in the nesting cycle but could not adequately provide for them after their first clutches hatched, at which time they switched to favoring their first females and broods. The large distances between primary and secondary nests, and the provisioning behavior of males, suggest that polygynous males were polyterritorial and deceived secondary females into pairing with them. For their part, about 70% of female Boreal

Owls in Europe abandon their families toward the end of the nestling period, at which time males are the sole caregivers until the young attain independence. Small numbers of deserting females re-nest with a different male, thereby increasing their annual productivity. In all but one case, polyandry occurred during the increase phase of the vole cycle.

Space limitations preclude discussion of the many other interesting topics covered in this book, including the effect of food abundance on nest initiation, clutch size, annual fledgling production, lifetime reproductive success, natal and breeding dispersal, survivorship, and mortality factors. In short, *The Boreal Owl* is a treasure trove of data presentation and thoughtful interpretation of results on just about any aspect of owl ecology you could imagine. Its value is further enhanced by the detailed discussions of the literature on a large number of other raptor species, and by discussions on studies of Boreal Owls throughout the rest of the species' range. As a single publication devoted to one species of owl, I believe it has no equal. Indeed, the only publication that comes close, in my mind, is the superb monograph on Long-eared Owls by Harry Wijnandts (1984, Ardea 72:1–92).

The two criticisms I have about the book involve the publisher. First, the quality of the printing on my copy is rather poor, with some of the text being so light that it is difficult to read. Second, the writing is not crisp, which sometimes required me to reread a passage multiple times to be sure I understood what the authors were trying to convey. This is not the fault of the authors, both of whom have published extensively in English, but neither of whom is a native speaker. Surely, Cambridge University Press should have taken the lead in editing the text carefully, thereby fully supporting the value of such an extraordinary body of work. I doubt many people will open *The Boreal Owl* and read it cover to cover, for it contains so large a range of topics, and covers them so thoroughly, that it obliges the reader to pause, reflect, and re-read various passages, in addition to flip back and forth between the text and the literature citations. Without question, however, it is a book that anyone with a keen interest in owls and life-history theory will value highly and consult often. It belongs in all research libraries and on the desks and book shelves of anyone who has ever been captivated by the publications of Erkki Korpimäki and his students and colleagues.—JEFFREY S. MARKS, 4241 SE Liebe Street, Portland, OR 97206, USA; e-mail: jeff17_marks@msn.com

DRAWN FROM PARADISE. By David Attenborough and Errol Fuller. Harper Design (an imprint of HarperCollins Publishers), 10 E. 53rd St, New York, New York, USA. 2012: 256 pages. ISBN: 978-0-0622-3468-1. $45.00 (hardcover).—The 21st century is a deeply satisfying time to be an ornithologist, a naturalist, a curious person. The resources now available to us in print, digital images and video, simply astound. To read David Attenborough and Errol Fuller's book, *Drawn from Paradise,* is to fully appreciate this fire hose flow of information, able to be summoned up with the twitch of a finger. As much as it is anything, the book is a tale of slow and painstaking exploration, specimen collecting, and supposition—much of it fanciful—about the most spectacular and bizarre birds on earth, the Paradisaeidae, which happen to live on one of earth's most spectacular and bizarre islands: New Guinea.

Luigi Maria D'Albertis, one of the many explorers vividly portrayed, remarked that in his view it was easier to cross the Alps than ascend one ordinary hill in Papua. It is in this mist-shrouded, hazard-strewn and deeply dangerous place that mystery thrives, that a family of birds seemingly too ornate to be possible diversified into a grab-bag of feather and behavioral specialization that elicits awe and disbelief.

That early specimens had wings and feet removed prior to shipping to Europe gave rise to fabulous tales (they flew without wings, and drank rain from the clouds) and bemusing attempts at illustration. In most early depictions of their dried skins, the artists faithfully reproduced the preparators' every misdeed and error, producing images that resemble flying tube socks, festooned with lacy filigree. Hauntingly recognizable bits crept into portraits in the early 17th century, decorating the hats of the royals; from their forbidding mountain fastnesses, pieces of these birds were finding their way into worldwide trade. It's all the more amazing, given the demand for their feathers, that so many species still survive—a testament to New Guinea's fortress.

Drawn from Paradise is illustrated entirely with paintings and drawings, with an impressive array ranging from 16th century woodcuts, to quick sketches by Rembrandt van Rijn, on through the spirited paintings of Joseph Wolf and Joseph Smit, the remarkably vibrant if understandably inaccurate renderings of Jacques Barraband, and the modern-day depictions of Australian painter William Cooper and *National Geographic* illustrator Walter

Ferguson. Cooper's pencil sketches of the birds as observed in life are gems. Some of the most arresting images in the book belong to contemporary painters Raymond Ching and co-author Errol Fuller, each bearing an elegiac rather than strictly descriptive quality that leaves a lingering mood.

The book is organized historically as well as taxonomically, describing the genera in the order that they were brought to light. A final chapter describes some of the birds' outlandish displays. Seized by a desire to witness them, a reader may now turn to birdsofparadiseproject.org. Only upon viewing the video clips of bird of paradise displays, made through enormous effort and multiple expeditions by photojournalist Tim Laman and evolutionary biologist Ed Scholes, can one understand how little we can know of a bird from its dried skin. Shooting a bird gives us a specimen that can last for centuries, but the knowledge we can gain from it only goes so far. For it is the power of life, hundreds of follicular muscles, and surging testosterone that transforms birds with bizarre and colorful feathers into glowing plates, discs, ellipses, comets, even leering psychedelic space aliens. Read *Drawn from Paradise.* Peruse the paintings, the various and largely unsuccessful attempts to figure out just how all those feathers might be employed in life. Then treat yourself to some videos of displaying birds. Sudden intakes of breath will progress to startled barks of laughter and incredulity as the birds of paradise vibrate, bounce, fluoresce and shape-shift beyond any mere human's capacity to anticipate or understand. Life is the thing; life is what was missing for so many centuries in our understanding of these birds. Field ornithology brings us the living bird, and for that, and for our newfound means of transmitting and consuming these images, *Drawn from Paradise* can only make us thankful.—JULIE ZICKEFOOSE, 330 Scotts Ridge, Whipple, OH 45788, USA; e-mail: julie@juliezickefoose.com

The Wilson Journal of Ornithology 125(4):860, 2013

THE BIRDS OF ALEXANDER WILSON-WILSON'S PLOVER (*CHARADRIUS WILSONIA*)

On 13 May 1813, Wilson shot an odd looking plover on the beach of Cape Island, New Jersey. It was his last trip to southern New Jersey, a much needed respite after months of intense work. Since his return to Philadelphia from his seven-month, western collecting trip in 1810, Wilson had researched, written, illustrated, edited, and produced volumes 3–7 of *American Ornithology*. He was preparing the illustrations and species accounts for volume 8 when he shot the plover. He and George Ord, his companion, determined that the plover was an undescribed species. They collected two males and a female. While preparing the specimens for Peale's museum, Wilson found the female's oviduct to be "greatly enlarged, and containing an egg half grown, apparently within a week of [laying]." He and Ord concluded that the species bred in the area and noted that the plover's "favorite places of resort appear to be the dry sand flats on the seashore." Wilson painted the plover as one of several birds found along the shore, but died on 23 August 1813 before writing a description. George Ord wrote the species account and named the plover after his friend whose illustration he used in volume 8. Wilson's Plover was the first species to commemorate Alexander Wilson's monumental contribution to American ornithology.

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THE BIRDS OF ALEXANDER WILSON-WILSON'S WARBLER (*CARDELLINA PUSILLA*)

"This neat and active little species I have never met with in the works of any European naturalist." With those words Wilson introduced the Green Black-capped Flycatcher (*Muscicapa pusilla*) to the world. He aptly described its habitat as "... almost unapproachable thickets in deep morasses...," which leaves one to marvel that he was able to collect specimens on which to base his detailed descriptions of both male and female.

Wilson's classification of this species as a *Muscicapa* reflected his reluctance to create new genera. Linneaus' influence was such that many of the naturalists who followed him were reluctant to alter his taxonomic organization and preferred to squeeze new species into an existing Linnaean genus and family. As new species accumulated and genera became unwieldy collections of disparate species, Lineaus' taxonomic system seemed in danger of collapsing into chaos. The ornithologist Lucien Bonaparte was among the first to break with precedent when he created new genera and families in his 1838 edition of Wilson's *American Ornithology*. Among other innovations he moved the Green Black-capped Flycatcher into the warblers, renamed it Wilson's Warbler, and placed it in the genus *Wilsonia*. Two years later Thomas Nuttall retained the common name, but placed the species in the genus *Sylvania* where it remained until 1910 when the 3rd edition of the AOU checklist resurrected the genus *Wilsonia* and placed Wilson's Warbler in the genus along with the Canada Warbler (*Cardellina canadensis*) and Hooded Warbler (now known as *Setophaga citrina*). In the 53rd supplement to the 7th edition of the checklist the genus *Wilsonia* was disbanded and Wilson's Warbler moved to the genus *Cardellina*. Is that the last word on Wilson's Green Black-capped Flycatcher?

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ERRATA

In Anthony et al. 2013, we mistakenly claimed (p. 307–308) that there were "no other reports" about post-fledging biology in Grasshopper Sparrows, and our paper was the "first quantitative report on fledgling activity in a migratory emberizine …". Prior to the publication of our paper, two publications, Hovick (2010) and Hovick et al. (2011), reported detailed comparisons of the survival of fledgling Grasshopper Sparrows tracked by telemetry in Iowa grasslands managed by fire and grazing. They reported rates of mortality (74%) of fledgling Grasshopper Sparrow mortality that match our report of 25% survival without telemetry in MD, the probable predators (and other causes) of the mortality, and the distances from the nest at which corpses and live juveniles were last detected. We acknowledge the precedence in publication of post-fledging Grasshopper Sparrow biology by Hovick (2010) and Hovick et al. (2011) and the citations within.

ANTHONY, T., D. E. GILL, D. M. SMALL, J. PARKS, AND H. F. SEARS. 2013. Post-fledging dispersal of Grasshopper Sparrows (*Ammodramus savannarum*) on a restored grassland in Maryland. Wilson Journal of Ornithology 125(2):307–313.

HOVICK, T. J., J. R. MILLER, R. R. KOFORD, D. M. ENGLE, AND D. M. DEBINSKI. 2011 (May). Post-fledging Survival of Grasshopper Sparrows in grasslands managed by fire and grazing. Condor 113(2):429–437.

HOVICK, T. J. 2010. Survival of Grasshopper Sparrows (*Ammodramus savannarum*) during two important life stages in grassland managed with fire and grazing. Master of Science Thesis. Wildlife Biology, Iowa State University, Ames, USA.

In Pugesek et al. 2013, the equation used to calculate yearly measures of juvenile and adult Whooping Crane (*Grus americana*) mortality in relation to blue crab abundance was not correct. The correct equation is:

$$Y = \beta_o\left(0.1 + e^{-\beta_1 * X}\right)$$

PUGESEK, B. H., M. J. BALDWIN, AND T. STEHN. 2013. The relationship of blue crab abundance to winter mortality of Whooping Cranes. Wilson Journal of Ornithology 125:658–661.

The Wilson Journal of Ornithology 125(4):862–879, 2013

PROCEEDINGS OF THE NINETY-FOURTH ANNUAL MEETING

JOHN A. SMALLWOOD, SECRETARY

The Ninety-fourth Annual Meeting of The Wilson Ornithological Society was held from Thursday, 7 March, through Sunday, 10 March, 2013, on the campus of the College of William & Mary, Williamsburg, Virginia. Daniel A. Cristol, Professor of Biology at the College of William & Mary, chaired the Committee on Local Arrangements, which also included John Swaddle, Matthias Leu, and Bryan Watts. The Williamsburg Bird Club graciously served as a local sponsor.

The Council met from 0901 to 1605 EST on Thursday, 7 March, in the Colony Room at the Sadler Center. That evening there was an ice-breaker social for the conferees and guests in Chesapeake Room A of the Sadler Center.

The scientific program began on Friday morning with the 2013 Margaret Morse Nice Plenary Lecture, delivered by the 2013 Margaret Morse Nice Medal recipient, Edward H. Burtt, Jr., and titled "From passion to science to the evolution of avian color." On Saturday morning Peter R. Grant and B. Rosemary Grant, the 2012 Margaret Morse Nice Medal recipients, presented the 2012 Margaret Morse Nice Plenary Lecture, titled "A long term study of Darwin's finches."

In addition to the plenary lectures, the scientific program included 153 presentations organized into 14 general sessions, 2 symposia on birds and human health and on aspects of the history and future of American ornithology from the perspective of The Wilson Ornithological Society on the occasion of its 125th anniversary, and 63 posters.

The Local Committee hosted field trips to local birding spots on Friday and Saturday morning. Conferees attended longer field trips on Sunday. Mike Wilson led a group to Piney Grove to observe Virginia's only Red-cockaded Woodpecker (*Picoides borealis*) nesting site. Dan Cristol led a group to Chincoteague National Wildlife Refuge with stops along the Eastern Shore. Another group, led by Harry Armistead, looked for birds at four Chesapeake Bay Bridge-Tunnel "islands" which had not been accessible to birders in recent years. Finally, Brian Tabor led a fourth group to Hog Island Wildlife Management Area.

On Saturday evening the conferees enjoyed a social gathering prior to the annual banquet. The evening events included dinner and afterwards WOS President Robert C. Beason, on behalf of all assembled, offered gratitude to the Local Committee for a successful conference. President Beason thanked the three elected members of Council who had completed their terms of office, Mark E. Deutschlander, Timothy J. O'Connell, and Becca Safran, and welcomed the three newly elected members of Council, Kerri Cornell Duerr, Letitia M. Reichart, and Peter G. Saenger. President Beason also congratulated the newly elected WOS President Robert L. Curry, whose term would begin at the close of the meeting, and gave to him the WOS ceremonial presidential gavel. The following WOS awards and commendations also were presented at the banquet:

2012 MARGARET MORSE NICE MEDAL

(for the WOS plenary lecture; presented in 2013)

Peter R. and Rosemary Grant, "A long-term study of Darwin's Finches."

2013 MARGARET MORSE NICE MEDAL

(for the WOS plenary lecture; also presented in 2013)

Edward H. Burtt, Jr., "From passion to science to the evolution of avian color."

EDWARD'S PRIZE

(for the best major article in volume 124 of *The Wilson Journal of Ornithology*)

Storrs L. Olson, "History, structure, evolution, behavior, distribution, and ecology of the extinct Hawaiian genus *Ciridops* (Fringillidae, Carduelini, Drepanidini)."

STORRS L. OLSON PRIZE

(for the best book review in volume 124 of *The Wilson Journal of Ornithology.*)

Ellen Paul, "The feathery tribe," by Daniel Lewis.

WILLIAM AND NANCY KLAMM SERVICE AWARD

(for distinguished service to The Wilson Ornithological Society)

Clait E. Braun.

LOUIS AGASSIZ FUERTES AWARDS

Karan Odom, "Why duet? A comparison of female songs and duets in a tropical songbird."

Andrew Rush, "The role of innate song in species recognition in a clade of *Empidonax* flycatchers."

GEORGE A. HALL/HAROLD F. MAYFIELD AWARD

William Clark, "Interbreeding between Harlan's Hawk (taxon *harlani*) and Red-tailed Hawk (taxon *jamaicensis*) in western Canada."

PAUL A. STEWART AWARDS

Amanda Arredondo, "Songs along the border: responses to playback at and beyond the leading edge of the northward-moving hybrid zone between Black-capped and Carolina chickadees."

Sarah Baillie, "Boldness in response to predatory threat and its correlation with reproductive success in Carolina Chickadees."

Christine Eldredge, "Parental attentiveness, dominance ranking, and feeding patterns in Carolina Chickadees (*Poecile carolinensis*): a field study of components of songbird behavior."

Jason Fischer, "The impact of urbanization on daily feeding activity: a test of foraging theory."

Morgan Harris, "The influence of competition on the expression of personality traits, assortative mating, and reproductive success: an experimental field study."

William Lewis, "Response of gut microbiota to long-distance passerine migration."

Henry Pollock, "Avian microclimate selectivity and climate change: a comparative approach."

Alex Wang, "Source and sink or ecological trap? Using juvenile dispersal of an endangered Hawaiian bird to tell the difference."

ALEXANDER WILSON PRIZE

(for best student paper)

Daniel Baldassarre, "Experimental evidence of asymmetrical introgression of a sexual trait via extra-pair mating."

Olga Milenkaya, "Testing the Condition-Quality Hypothesis: condition indices are repeatable but do not predict reproductive success or survival."

LYNDS JONES PRIZE

(for best student poster presentation)

Jessica Benson, "Mercury exposure results in hyperactivity and decreased neophobia in Zebra Finches."

NANCY KLAMM BEST UNDERGRADUATE STUDENT ORAL PAPER AWARD

Rachel Hebert, "The process of fledging in the Mountain Bluebird (*Sialia currucoides*)."

Felicia Napolillo, "Variation in incubation effort during egg-laying in the Mountain Bluebird and its association with hatching asynchrony."

NANCY KLAMM BEST UNDERGRADUATE STUDENT POSTER AWARD

Oliver Muellerklein, "Territoriality and spatial dynamics in Grasshopper Sparrows: a mathematical model."

WOS STUDENT TRAVEL AWARDS

Jacob Armiger, "Group composition and site-fidelity in the facultatively cooperative Yucatan Wren (*Campylorhynchus yucatanicus*)."

Sarah Baillie, "Boldness in response to predatory threat in Carolina Chickadees (*Poecile carolinensis*)."

Rachel Bellis, "Age ratios, condition, and productivity of Lake Erie Islands breeding birds."

Anna Brownson, "Mate choice vs. mate guarding: the behavioral aspects of reproductive skew in Acorn Woodpeckers (*Melanerpes formicivorus*)."

Corey Callaghan, "Latency in Magnolia Warbler flight calling behavior."

Andrew Dennhardt, "Modeling migratory flight routes of raptors in variable meteorological and topographic landscapes."

Christine Eldredge, "Deadbeat dad… or mom? Patterns of parental attentiveness in Carolina Chickadees (*Poecile carolinensis*)."

Erin Feichtinger, "Associations of Scissor-tailed Flycatchers (*Tyrannus forficatus*) with specific land-cover types in south-central Texas."

Natasha Hagemeyer, "Incomplete song divergence between the recently diverged Orchard and Fuertes' orioles."

Amanda Hagstrom, "Stressed or chill? Response of nestling Red-winged Blackbirds to a perceived stressful event."

Rachel Hebert, "The process and cause of fledging in the Mountain Bluebird."

Erin Heller, "Effects of urbanization on the relationship among birds, ticks, and tick- borne diseases."

Samantha Higgins, "Do House Sparrows (*Passer domesticus*) adjust parental care behaviors when mates desert? A test of the Negotiation Rule."

Nathan Hillis, "Nest success of Western Kingbird on a university campus."

Aymen Hussein, "Song characteristics of the critically endangered Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*)."

Evan Kelemen, "Singing behavior in Carolina Chickadees (*Poecile carolinensis*) is consistent across contexts."

Chris Latimer, "Avian community dynamics in response to vegetation restoration on reclaimed surface-mines in southwest Virginia."

Ari Martinez, "Are mixed-species bird flocks stable through two decades?"

Olga Milenkaya, "Testing the Condition-Quality Hypothesis: condition indices are repeatable but do not predict reproductive success or survival."

Adrian Monroe, "Dickcissel nest success in native warm-season grass pastures: effects of vegetation structure and weather."

Felicia Napolillo, "Variation in incubation effort during egg-laying in the Mountain Bluebird and its association with hatching asynchrony."

Abbey Ramirez, "Habitat selection of nesting Mississippi Kites in Oklahoma Cross Timbers."

Michelle Stretch, "Comparison of baseline levels of corticosterone between male and female nestling Red-winged Blackbirds."

Rachel Thomas, "Antibacterial action of unusual pigments on unusual birds."

Brian Treveline. "DNA barcoding: a molecular technique for determining diet composition from fecal sacs of Louisiana Waterthrush."

Cassie Volker, "Continuous remote monitoring of nest attendance by incubating female Carolina Chickadees."

Maria Wheeler, "The genetic impact of translocations and reintroduction: a tale of two eagles."

Stephanie Wright, "Ward revisited: variation in Carolina Chickadee song across its range."

Selection Committee for the Nice Medal: E. Dale Kennedy (Chair), Robert C. Beason, Robert L. Curry, and Sara R. Morris; for the Edwards Prize: Clait E. Braun (Chair), Morton L. Isler, and Storrs L. Olson; for the Olson Prize: Clait E. Braun (Chair), Storrs L. Olson, and Mary Bomberger Brown; for the Klamm Service Award: Sara R. Morris (Chair), Richard C. Banks, Charles R. Blem, Leann Blem, Jerome A. Jackson, and Doris J. Watt; for the Fuertes, Hall/Mayfield, and Stewart Awards: Jameson F. Chace (Chair), Eric Atkinson, William H. Barnard, Carla J. Dove, Laurie J. Goodrich, Margret I. Hatch, Kamal Islam, Jason Johnson, Robert Mulvihill, Shane Pruett, Scott Robinson, Steven Schoech, Daniel Shutack, Marc Stanback, Travis Wilcoxen, and Douglas W. White; for the Alexander Wilson Prize, the Lynds Jones Prize, and the Nancy Klamm undergraduate presentation awards: Robert L Curry (Chair), Luke Butler, Jameson F. Chace, Mark E. Deutschlander, Adam E. Duerr, Kerri Cornell Duerr, Chris Goguen, Margret I. Hatch, Mark E. Hauber, Douglas A. James, L. Scott Johnson, E. Dale Kennedy, Jeremy Kirchman, John C. Kricher, Mattias Leu, Bernie Lohr, Sarah Mabey, John E. Quinn, Claire Varian Ramos, Letitia M. Reichart, Dennis G. Siegfried, Jeffrey Stratford, Caz M. Taylor, Todd J. Underwood, Lindsey Walters, Doris J. Watt, Douglas W. White; and for the WOS Student Travel Awards: Mark E. Deutschlander (Chair), William H. Barnard, Edward H. Burtt, Jr., Kristen Covino, Robert L. Curry, Jack Eitniear, Margret I. Hatch, Mark E. Hauber, Todd E. Katzner, Daniel Klem, Jr., Dennis G. Siegfried, Sue Smith-Pagano, Lindsey Walters, and Douglas W. White.

COMMENDATION

WHEREAS THE WILSON ORNITHOLOGICAL SOCIETY held its 2013 annual meeting in historic Williamsburg, Virginia, at the invitation of the correspondingly historic College of William & Mary,

RECOGNIZING that the Committee on the Scientific Program, under the skillful direction of Sara R. Morris, assembled an outstanding schedule of oral and poster presentations, which included a special symposium on the history and future of American ornithology from the perspective of The Wilson Ornithological Society on the occasion of its 125th anniversary, and two superb Margaret Morse Nice plenary lectures, by Jed Burtt, and by Peter and Rosemary Grant, and

RECOGNIZING that the Committee on Local Arrangements, under the able direction of Daniel A. Cristol, provided an excellent conference venue with comfortable accommodations and interesting bird watching opportunities, and

WHEREAS the conferees found this meeting both informative and enjoyable,

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society commends the Committee on the Scientific Program, the Committee on Local Arrangements, and the local

sponsors for a most successful and rewarding meeting in historic Williamsburg.

COMMENDATION

WHEREAS Robert C. Beason has faithfully and conscientiously served as President of The Wilson Ornithological Society during our historic 125th year,

RECOGNIZING that he presided over the recruitment and election of our Society's first female Editor, and

RECOGNIZING his leadership in navigating through uncertainty and change in ornithological societies, and ensuring continuation of The Wilson Ornithological Society's unique role in American ornithology, and

RECOGNIZING his remarkable ability to conduct effective meetings in which Council reaches consensus through thoughtful deliberation, yet completes its business ahead of schedule,

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society enthusiastically offers its sincere gratitude to Bob Beason for a job extraordinarily well done.

COMMENDATION

WHEREAS Clait E. Braun has served The Wilson Ornithological Society in the capacity of Editor of *The Wilson Journal of Ornithology* for the past six years, with the indispensable assistance of Nancy Braun, and

WHEREAS through his remarkable editorial skills he has advanced the reputation of *The Wilson Journal of Ornithology* as one of the premier journals of ornithology, and

WHEREAS through his steady leadership he has guided the *Journal* through the changing environment of scientific publication, and

WHEREAS through their relentless efforts, Clait and Nancy have consistently produced a top-tier publication, delivered on schedule,

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society expresses its deepest and heart-felt appreciation to Clait and Nancy Braun and for their many years of commitment and service to their Society.

BUSINESS MEETING

President Robert C. Beason called the Annual Business Meeting to order at 1705 Friday, 8 March 2013, in the Commonwealth Auditorium, College of William & Mary. As the number of members that had gathered significantly exceeded the required quorum of 25, President Beason introduced Secretary John A. Smallwood, who summarized for those gathered what had taken place the previous day at the Council Meeting. At the end of 2012, the Society's membership stood at 1,598 individuals, including 259 students. In addition, exactly 300 libraries and institutions subscribed to *The Wilson Journal of Ornithology*. Secretary Smallwood then asked those assembled to stand in recognition of the following members who were recently deceased: Guy Baldassarre (Tully, NY), Donald M. Bradburn (New Orleans, LA), John W. Hardy (Gainesville, FL), Pershing Hofslund (Duluth, MN), M. Philip Kahl (Sedona, AZ), and Peter Stettenheim (Lebanon, NH).

Secretary Smallwood reported that the Society enjoys an excellent financial position, with an endowment of over $2,700,000, an increase of over $200,000 during the previous year, and that the endowment continues to increase in value as the market improves. On behalf of Council, the Secretary offered sincerest gratitude to the WOS Finance, Audit, and Investment Committee, chaired by Allan R. Keith, for its astute management of the Society's assets. On a sad note, Secretary Smallwood reminded the members that Peter Stettenheim had been a long-serving member of the committee, and will be missed.

Secretary Smallwood then introduced the Chair of the WOS Research Awards Committee, Jameson F. Chace, who announced two new research awards that Council had approved. Beginning in 2014, the Society will grant up to four Wilson Ornithological Society Research Awards, $1,500 each, for study in any area of ornithology. At least two of these grants will be awarded to master's students. Also beginning in 2014, the Society will offer two Wilson Undergraduate Mentoring Awards of $3,000 each. These awards include $1,000 for research and up to $1,000 each to the student and mentor to help defray the cost associated with attending a subsequent WOS annual meeting to present the results of the funded project.

Treasurer Melinda M. Clark then presented the Treasurer's report, which is included in these Proceedings, below. Subsequently, Clait E. Braun, retiring Editor of *The Wilson Journal of Ornithology*, presented his final Editor's Report (included below) and received expressions of well-deserved appreciation for such outstanding service. The new Editor of *The Wilson Journal of Ornithology*, Mary Bomberger Brown, presented a report of her editorial activities (below)

regarding the production of *WJO* Volume 125. On the previous day Council had unanimously and enthusiastically re-elected Editor Brown to her next 1-year term as Editor.

Timothy J. O'Connell, Chair, presented the report of the Nominating Committee, in which the following slate of candidates were offered: President, Robert L. Curry; First Vice-President, Sara R. Morris; Second Vice-President, Mark E. Deutschlander; Secretary, John A. Smallwood; Treasurer, Melinda M. Clark; and members of Council for 2013–2016 (three nominees for three positions), Kerri Cornell Duerr, Letitia Richart, and Peter G. Saenger. Having asked for additional nominations from the floor and hearing none, Chairperson O'Connell closed the nominations as a result of a motion by Jerome A. Jackson, seconded by E. Dale Kennedy, which was passed unanimously by acclamation. Richard C. Banks wasted no time to move that the Secretary cast a single unanimous vote for the slate of nominees. This motion was seconded by Joseph R. Jehl, Jr., and again by acclamation, it became so.

Next, Jameson F. Chace, Chair of the Committee on Local Arrangements for the 2014 Annual Meeting, updated those assembled on our next meeting, to be held at Salve Regina University in Newport, Rhode Island, 29 May to 1 June. First Vice-President Robert L. Curry then informed the members about the preparations underway to hold the 2015 meeting jointly with the Society of Canadian Ornithologists/Société des Ornithologistes du Canada at Acadia University in Wolfville, Nova Scotia, 16 to18 July. Dave Shutler will chair the Local Arrangements Committee.

Following an announcement by Mark E. Deutschlander, Chair of the WOS Student Travel Awards Committee, regarding the distribution of travel award checks, and having completed the agenda of the Business Meeting, President Beason inquired if anyone present had further items of business. Because no one did, Robert L. Curry moved and Timothy J. O'Connell seconded that we adjourn. And by the third voice acclamation of this assembly, it came to pass at 1724.

REPORT OF THE TREASURER

WILSON ORNITHOLOGICAL SOCIETY
Statement of Position
31 December 2012

ASSETS		**2012**
Cash Investments:		
Merrill Lynch - cash	$	102,036
Coamerica - Van Tyne checking		280
Van Tyne Univ Michigan account and PayPal		711
Wilson Editorial bank account		260
Sutton Fund - cash equivalents		17,757
Howland Mgmt - cash equivalent		30,508
Total cash and cash equivalents		151,552
Other Investments:		
Merrill Lynch - common stocks		315,333
Merrill Lynch - corp bonds and alternative investment		19,340
Merrill Lynch - mutual funds		512,455
Sutton Fund - equities		159,059
Sutton Fund - corp bonds		-
Howland Mgmt - equities		1,245,142
Howland Mgmt - fixed income		352,112
Total Other Investments		2,603,441
Total Assets	$	2,754,993
FUND BALANCES		
Fund Balances:		
Restricted funds - Sutton Fund	$	176,816
Unrestricted funds		760,922

Net Income	189,493
	950,415
Fund balance - Klamm	1,627,762
Total Fund Balances	$ 2,754,993
FUND BALANCES	

WILSON ORNITHOLOGICAL SOCIETY
Statements of Revenues and Expenses
For the Year Ending December 31, 2012
Budgets for the Years Ended December 31, 2013 and 2012

	2012 12 Months Actual	2012 Annual Budget	2013 Annual Budget
Revenues			
Contributions	$ 231	$ 1,000	$ 1,000
Student Travel Research Fund	353	500	500
Van Tyne Library Book Fund	110	110	110
Sales - back issues	316	200	200
Sales - books - Van Tyne Libr.	-	100	100
Subscriptions	7,680	10,000	9,000
Page charges	28,911	30,000	30,000
Royalties	9,197	17,000	8,800
BioOne Electronic Licensing	36,884	26,000	36,000
Mailing list rental income	153	300	300
Memberships	31,867	40,000	40,000
Other income	120		500
Total revenues from operations	115,822	125,210	126,510
Expenses			
Bulletin publication costs:			
Editorial honorarium	15,000	15,000	15,000
Editor travel	1,419	1,350	1,350
Editor supplies/Mailings	3,463	3,000	3,000
Editorial assistance	28,780	23,000	23,000
Office start up costs		30,000	2,000
Printing - bulletin	94,992	90,000	92,000
Artwork	250	750	750
Printing color plates	3,416	3,600	3,600
	147,320	166,700	140,700
Operating expenses:			
Postage & mailing - back issue	-	500	150
Storage back issues	285	750	360
Van Tyne Library - expenses	942	1,600	1,000
OSNA management services	14,736	15,000	15,000
Credit card fees	2,842	4,100	3,000
Travel expenses-OSNA rep		500	500
Travel expenses - general and Treasurer	968	6,500	1,500
Travel expenses-Ornith Council	14	250	250
Meeting expenses	11,685	5,000	5,000
Membership expenses		2,000	2,000
Accounting fees	4,199	4,500	4,500
Tax preparation fees		1,000	1,000
Insurance - D&O	1,623	1,600	1,600

Office supplies	**378**	305	305
Postage - general		200	200
Other expenses	**310**	100	100
Filing fees	**10**	10	10
Discretionary expenses		3,000	3,000
	37,992	46,915	39,475
Awards:			
Student banquet	**554**	1,200	1,200
Membership awards		600	600
Hall/Mayfield	**1,000**	1,000	1,000
Stewart	**7,300**	8,000	8,000
Fuertes	**2,500**	5,000	5,000
Klamm service award		1,000	1,000
Wilson, Lynds Jones, Klamm	**700**	700	700
Student travel grants	**15,000**	10,000	7,500
Award expenses	**1,118**	2,553	3,553
	28,172	30,053	28,553
Contributions:			
Support - Ornith Council	**15,000**	15,000	15,500
AAZN dues		250	250
	15,000	15,250	15,750
Total Expenses	**228,484**	258,918	224,478
Expenses in excess of revenues before investment income	**(112,662)**	(133,708)	(97,968)
Investment activity:			
Revenues			
Realized gain/loss - ML	**304,801**		
Realized gains/losses-Howland	**182,486**		
Realized gains/losses - Sutton	**55,212**		
Unrealized gain/loss - ML	**(235,553)**		
Unrealized gain/loss - Howland	**(14,454)**		
Unrealized gain/loss - Sutton	**(42,980)**		
Investment earnings - ML	**26,007**		
Investment earnings - Howland	**39,638**		
Investment earnings - Sutton	**12,865**		
Total revenues from investment activity	**328,022**	220,000	115,000
Investment fees	**25,867**	25,000	26,000
Investment revenues in excess of expenses	**302,155**	195,000	89,000
Total revenues in excess of expenses	$ **189,493**	$ 61,292	$ (8,968)

Melinda M. Clark, *Treasurer*

EDITOR'S REPORT (VOLUME 124, 2012)

This report is for 2012 (Volume 124), my last in the 6-year period (2007–2012). All four Issues were published on time and the Volume contained 878 pages, including 118 articles, as well as 15 Book Reviews, three Editorials (News), one Award, one Memorial, the Proceedings of the Annual Meeting, list of Reviewers, and the Index. The published material also included current listings of the winners of the major awards and Annual Meeting locations to fill blank pages as needed.

We (Nancy and I) continued to receive and assign manuscripts for review through 30 June after which all new manuscripts were electronically sent to the Editor for 2013, Mary Bomberger Brown. Manuscripts still in the system were edited in the Tucson, Arizona, office as they arrived. All lingering authors were repeatedly encouraged to return their revisions to us as soon

as possible or to make a decision to withdraw their submissions. Mary visited our office in May to learn the systems that worked for us. Our final issue (Dec) was made up and sent to Allen Press in early September. We then started sending edited copy awaiting Issue make up of possibly acceptable manuscripts electronically (the paper files were mailed) to the editorial office in Lincoln, Nebraska. This process was essentially completed by 1 October. Nancy sent the page charge invoices for the December Issue to authors once the Issue was mailed. We continued to encourage those with outstanding page charges whenever prompted by Treasurer Melinda M. Clark through the end of December. Nancy also updated the list of reviewers accumulated over the 6-year period as to their willingness to continue to review and adding Key Words. This process was completed by late January 2013 when the final listing (Excel file) was sent to Editor Mary Bomberger Brown.

My last activity was to form the committees to review papers published in Volume 124 to select the Edwards Prize winner for the Best Paper and Olson Prize for the Best Book Review. This was completed in January 2013 and those awards will be announced and presented at this meeting.

Nancy and I are pleased to have served as the editorial team for the *Wilson Journal of Ornithology* for 2007–2012. These 6+ years have gone by quickly and we had little spare time. We thank the Authors, Reviewers, Indexers, Book Review Editors, Editorial Board, and WOS Council for helping produce a quality Journal.

Clait E. Braun, *Editor*

EDITOR'S REPORT (VOLUME 125, 2013)

In 2012, 197 manuscripts were submitted for publication in *The Wilson Journal of Ornithology*. Manuscripts 1–108 were submitted to the editorial office based in Tucson, AZ, and manuscripts 109–197 were submitted to the office in Lincoln, NE. Of these manuscripts, 169 have been resolved; of the manuscripts submitted to Lincoln, 32 have been accepted and 29 declined or withdrawn. Of the remaining 28 manuscripts, 18 are in revision, 4 are in review, and 6 are likely to be declined. From July–December 2012, the average length of time from receipt of a manuscript to first resolution (decline or return for revision) was 64.5 days (minimum = 30 days, maximum = 122 days). The average length of time from return for revision to acceptance was 37.3 days (minimum = 15 days, maximum = 50 days). And, the average number of reviews solicited per manuscript = 3.4 (2–8). Indispensable to this process were the efforts of Melissa J. Panella, who joined the *WJO* as Associate Editor.

We received manuscripts for review from corresponding authors based in Argentina, Bolivia, Brazil, Canada, Chile, China, Costa Rica, Hungary, India, Iran, Israel, Italy, Japan, Korea, Mexico, New Zealand, Norway, Poland, Russia, Singapore, Slovakia, Sweden, and the USA. The manuscripts were based on research conducted in Argentina, Bolivia, Brazil, Canada, China, Chile, Costa Rica, Ecuador, Germany, Hungary, India, Iran, Israel, Italy, Japan, Mexico, New Caledonia, Nicaragua, Norway, Peru, Puerto Rico, Russia, Singapore, Slovakia, Sweden, Tanzania, USA, and Venezuela.

We made several changes to how the editorial office manages manuscripts. All correspondence related to a manuscript (acknowledgment, review solicitation, review receipt, revision management, and page proofs) is managed electronically through e-mail, UNL Dropbox (a file transfer service), and Allen Press; no hardcopies are mailed or couriered and to date we have not received any requests for this type of communication. Corresponding authors are receiving annotatable PDF page proofs from Allen Press. Managing all editorial office activities electronically has allowed us to (1) save time for authors, reviewers, and editorial staff; (2) save money for the *WJO* and WOS by reducing operating expenses; (3) improve efficiency for the *WJO* and Allen Press; and (4) make the *WJO* more attractive to prospective authors. Several authors have commented that they like submitting manuscripts via e-mail rather than uploading through publisher portals, making the *WJO* more attractive to them. We select reviewers based on the *WJO* Reviewer List key words (list compiled by Nancy Braun), searches on Google Scholar, and professional recommendations. This combination strategy is broadening the geographic and conceptual scope of our reviewers. A positive consequence of this strategy is that we are contacting international reviewers who were previously unaware of the *WJO* and several have subsequently submitted manuscripts for review. The *Guidelines for authors* was revised, including the addition of key words and several stylistic changes, and placed online at http://wjoonline.org and http://www.wilsonsociety.org. We added a brief feature,

The birds of Alexander Wilson, by Edward H. Burtt, Jr., to accompany the pen-and-ink drawings that adorn the *WJO* cover.

We fulfilled requests from Professor Tim Birkhead, University of Sheffield, to (1) reprint figures from *The Wilson Bulletin* in a book to be coauthored with Wimpenny and Montgomerie, *Ten thousand birds: ornithology since Darwin*, to be published by Princeton University Press, and (2) provide photos of Olin Sewall Pettingill and Josselyn van Tyne for publication in a gallery of ornithologists in the same publication. We also fulfilled a request from the Open University of Israel to reproduce figures originally published in *The Wilson Bulletin* in a book, *Faunistics of terrestrial vertebrates: an Israeli view*, and we fulfilled a request from Tom Reaume to reproduce figures originally published in *The Wilson Bulletin* in an e-book on the natural history of the American Crow (*Corvus brachyrhynchos*). Finally, we fulfilled a request from Rare Bird Picture, Inc., a film production company, to provide copies of *The Wilson Journal of Ornithology* to help furnish an office that will be used in a film project about birding, *A birder's guide to everything*, directed by Rob Meyer and starring Ben Kingsley. This has potential to offer additional recognition of *The Wilson Journal of Ornithology* to an expanded audience.

Clait and Nancy Braun facilitated the transfer of the *WJO* editorial office from Tucson to Lincoln. In preparation for the transfer, Mary Bomberger Brown traveled to Tucson in May to discuss *WJO* operating procedures, Allen Press procedures, and other issues. Clait and Nancy provided enough accepted/copy-edited manuscripts to fill Volume 125, Issue 1, giving us time to establish our procedures and become settled in our positions. Clait and Nancy also contacted the corresponding authors of all manuscripts with well past due revision; a couple of these authors responded, and the manuscripts appeared in Volume 125, Issue 1. Nancy is updating the *WJO* Reviewer List with current e-mail addresses and key words. Whenever we have questions or concerns, Clait and Nancy graciously come to our aid and we are grateful for all their help.

We welcome questions, comments, suggestions, and other inquiries from the WOS Council, WOS members, *WJO* readers, and others to improve the quality and impact of the journal.

Mary Bomberger Brown, *Editor*

The reports of the standing committees are as follows:

REPORT OF THE UNDERGRADUATE OUTREACH COMMITTEE

The committee is updating and expanding the *Guide to graduate studies in ornithology in North America* which has been posted on the WOS web page since 2003. We reviewed information for all institutions in the last version of the *Guide* to produce a January 2013 updated listing of graduate advisors in ornithology at 46 institutions in 35 North American states and provinces. The *Guide* would be more useful to undergraduate college students and their academic advisors if it were more complete. To identify omitted graduate programs, we are reviewing ornithological society membership rolls and meeting programs.

Douglas W. White, *Chair*

REPORT OF THE JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE

Janet E. Hinshaw, WOS Librarian, has been in touch with me throughout the year and has provided information on library use that is appended below. The big news and concern at the moment is that the museum collections are going to be moved to a new building and space is going to be limited. There are some administrative forces apparently opposed to the library being housed with the collections. Janet will be located with the collections. There is a plan in the works for a new biology building for faculty, labs, graduate students, and the exhibit museum, but again, space for the library is not yet on the table. The current museum director says that for the time being we should "wait and see," but libraries are not much interested in non-digital materials anymore. Janet indicates that only about 10% of museum titles are digital at the moment.

Janet reported the following statistics for the Josselyn Van Tyne Memorial Library during 2012:

Acquisitions

Exchanges.—We received 119 publications by exchanges with 95 organizations or individuals.

Gifts.—We received 26 publications as gifts from 23 organizations.

Subscriptions.—We received 31 publications from 23 subscriptions, spending a total of $855 on subscriptions in 2012.

Donations.—Donations received included two books from John Weber.

Purchases.—The library purchased 1 cd, 15 journal volumes, and 6 monographs for $217 and 1 monograph for $45 credit from Buteo Books.

Dispersals

Sales.—Seventeen duplicate journal issues were sold, bringing in a total of $17.00.

Gifts to Other Institutions.—Two cartons of duplicate reprints were donated to Lloyd Kiff. Due to the impending move of the museum collections, we are trying to cut down on our duplicates. We currently are disposing of reprints from the major journals which are available online. We hope to reduce the size of the reprint collection by 30%. It currently takes up about 100 m of shelf space.

Use of Resources

During the past year 15 loans of 2 journal volumes and 1 reprint, and photocopies and scans of 14 articles were sent to 12 members. We remind members that we can lend books or provide paper or electronic copies of articles from items in the library.

Thank Yous

Thanks to Janet and her student library worker, Rachel Hillabrand, who assists with day-to-day operations and with photocopying.

Jerome A. Jackson, *Chair*

REPORT OF THE SCIENTIFIC PROGRAM COMMITTEE

The Committee on the Scientific Program was chaired by WOS Second Vice-President Sara R. Morris. Daniel A. Cristol organized the symposium on birds and human health, which was moderated by John Swaddle. Jerome A. Jackson organized the symposium on aspects of the history and future of American ornithology, which he also moderated. The general paper sessions were moderated by Lesley Bulluck, Adam E. Duerr, Kerri Cornell Duerr, Christopher B. Goguen, John E. Quinn, Claire V. Ramos, Letitia M. Reichart, Christina Riehl, Douglas H. Shedd, Christine D. Sheppard, Dennis G. Siegfried, Scott Stoleson, Lindsey Walters, and David Wiedenfeld.

PAPER SESSIONS

Symposium: Birds and Human Health

Daniel A. Cristol, College of William & Mary, "Birds as sentinels and models for the problem of mercury pollution."

Carla J. Dove, Smithsonian Institution Feather Identification Laboratory, "When birds collide."

Sylvia L. Halkin, Central Connecticut State University, "Northern Cardinals as victims, vectors, and sentinels for West Nile Virus."

Erin Heller, Eric Walters, and Holly Gaff, Old Dominion University, "The effects of urbanization on the relationship among birds, ticks, and tick-borne diseases."

Matthias Leu, Joanna Weeks, Matt Feresten, Christopher Tyson, Nora Wicks, Joseph Thompson, and Alan Harris, College of William & Mary, "Does anthropogenic forest fragmentation affect distributions of ticks, exotic plants, and deer?"

John P. Swaddle, College of William & Mary, "Increased bird diversity is associated with lower incidence of West Nile Virus infections in humans."

Eric L. Walters and Holly D. Gaff, Old Dominion University, R. Jory Brinkerhoff, University of Richmond, and Robyn M. Naldony, Old Dominion University, "The possible role of avian hosts in newly established populations of the Gulf Coast tick (*Amblyomma maculatum*)."

Joanna Weeks, Matthias Leu, Matt Feresten, and Oliver Kerscher, College of William & Mary, "Modeling tick-borne diseases in the changing landscape of the Virginian peninsula: a tool for urban planning in the context of human health."

Symposium: Aspects of the History and Future of American Ornithology

Edward H. Burtt, Jr., and Jack M. Stenger, Ohio Wesleyan University, "Alexander Wilson, the masterful author of American ornithology."

William E. Davis, Jr., Boston University, "The role of avocational birders in American ornithology and in The Wilson Ornithological Society."

Bette J. S. Jackson and Jerome A. Jackson, Florida Gulf Coast University, "Founders of The Wilson Ornithological Society: a gallery of kids, joiners, botanists, and friends in search of collaborators, knowledge, and the conservation of birds."

Jerome A. Jackson, Florida Gulf Coast University, "Dealing with crises: the power of diversity, friendships, collaboration, and individual persistence of professionals in the middle years of The Wilson Ornithological Society."

Shepard Krech, III, Brown University and the Smithsonian Institution, "Mark Catesby's birds."

John C. Kricher, Wheaton College, "The once and future Wilson Ornithological Society."

General Sessions

Caleb Arellano, Irby Lovette, Yula Kapetanakos, and Alan Poole, Cornell University, "Sex-

ratio bias in hatch order of a population of Ospreys (*Pandion haliaetus*)."

Jacob Armiger and Robert Curry, Villanova University, "Group composition and site-fidelity in the facultatively cooperative Yucatan Wren (*Campylorhynchus yucatanicus*)."

Sarah K. Baillie and Robert L. Curry, Villanova University, "Boldness in response to predatory threat in Carolina Chickadees (*Poecile carolinensis*)."

Daniel Baldassarre and Michael Webster, Cornell University, "Experimental evidence of asymmetrical introgression of a sexual trait via extra-pair mating."

Ethan P. Barton and Margaret Brittingham, Pennsylvania State University, "Local effects of Marcellus Shale natural gas drilling on north-central Pennsylvania forest birds."

Jacob L. Berl and John W. Edwards, West Virginia University, and Jeff S. Bolsinger, Fort Drum Military Installation, "Red-headed Woodpecker breeding ecology and habitat use at the northern limit of its range."

Dominic Bouvier and Dennis Siegfried, Southwest Baptist University, and Brad Jacobs, Missouri Department of Conservation, "Predicting species occurrence in a changing landscape: a case study of the families Cardinalidae and Thraupidae."

Carol L Brackett and Susan B. McRae, East Carolina University, "Genetic analysis of reproductive behavior in a coastal population of the King Rail."

Rebecka L. Brasso, Michael J. Polito, and Steven D. Emslie, University of North Carolina Wilmington, "Investigating the influence of diet and foraging habitat on mercury concentrations in Adélie Penguins in two geographically distinct Antarctic marine food webs."

Anna C. Brownson and Eric L. Walters, Old Dominion University, and Walter D. Koenig, Cornell University, "Mate choice vs. mate guarding: the behavioral aspects of reproductive skew in Acorn Woodpeckers (*Melanerpes formicivorus*)."

Lesley Bulluck, Virginia Commonwealth University, Sarah Huber, Virginia Institute of Marine Sciences, and Cathy Viverette and Charles Blem, Virginia Commonwealth University, "Prothonotary Warblers exhibit age-specific reproduction with regard to spring temperature."

Corey Callaghan, Kaitlin Garrity, and Sara Morris, Canisius College, and Amy Tegeler, Powdermill Avian Research Center, "Latency in Magnolia Warbler flight calling behavior."

Paul Callo, Mary Baldwin College, "Red-eyed Vireos and avian malaria: a long term study."

Mery Casady and Letitia M. Reichart, University of Nebraska Kearney, "Corticosterone levels in sub-adult and family groups of Whooping Cranes (*Grus americana*) in wintering locations of Lamar Peninsula, Texas."

Jameson F. Chace, Karafaye Buffa, and Gina M. Varuzzo, Salve Regina University, "Factors affecting the distribution and abundance of wintering sea birds along Newport Neck, Rhode Island."

Andrew J. Dennhardt, Todd E. Katzner, Adam E. Duerr, and George T. Merovich, Jr., West Virginia University, and David Brandes, Lafayette College, "Modeling migratory flight routes of raptors in variable meteorological and topographic landscapes."

Adam E. Duerr and Tricia A. Miller, West Virginia University, Michael Lanzone, Cellular Tracking Technologies LLC, Dave Brandes, Lafayette College, Jeff Cooper, Virginia Department of Game and Inland Fisheries, Kieran O'Malley, West Virginia Division of Natural Resources, Charles Maisonneuve, Ministère des Ressources naturelles et de la Faune, Rimouski, Québec, Junior Tremblay, Ministère des Ressources naturelles et de la Faune, Québec City, Québec, and Todd E. Katzner, West Virginia University and USDA Forest Service, "Meteorological drivers of soaring migratory flight of the Golden Eagles in eastern North America."

Jessica Ebers, College of William & Mary, "The effect of methylmercury on immune response to a common parasite in Zebra Finches."

Christine Eldredge and Robert Curry, Villanova University, "Deadbeat dad....or mom? Patterns of parental attentiveness in Carolina Chickadees (*Poecile carolinensis*)."

Camilo Escallón and Alex Tallant, Virginia Polytechnic Institute and State University, Winfried Wojtenek, Escuela Superior Politécnica Ecológica Amazónica, Tena, Ecuador, Elisa Bonaccorso, Universidad Tecnológica Indoamérica, Ecuador, and Ignacio T. Moore, Virginia Polytechnic Institute and State University, "Avian malaria, testosterone, and elevation in a tropical sparrow."

Erin E. Feichtinger, University of South Florida, and Joseph A. Veech, Texas State University, "Association of Scissor-tailed Flycatchers (*Tyrannus forficatus*) with specific land-cover types in south-central Texas."

Jim Fraser and Sarah M. Karpanty, Virginia Tech, Jonathan B. Cohen, State University of New York Syracuse, and Barry R. Truitt, The Nature Conservancy, "The Red Knot (*Calidris canutus rufa*) decline in the Western Hemisphere: is there a lemming connection?"

Meryl Friedrich, Dan Catlin, and Jim Fraser, Virginia Tech, "Mate retention and nest success in Piping Plovers (*Charadrius melodus*) on the Missouri River."

Nathan Fronk and Margaret Brittingham, Pennsylvania State University, "Effect of Marcellus Shale gas development on forest bird species in north-central Pennsylvania."

Katherina Gieder, Sarah Karpanty, Jim Fraser, and Dan Catlin, Virginia Tech, "Historical data on Piping Plover responses to storms and construction of a storm berm at Assateague Island National Seashore provide basis for modeling effects of future sea-level rise and altered storminess."

Christopher B. Goguen, Pennsylvania State University, "Nesting ecology of Veeries in habitats invaded by exotic shrubs in northeastern Pennsylvania."

Natasha D. G. Hagemeyer, Old Dominion University, Rachel J. Sturge, University of Maryland Baltimore County, J. Jordan Pride, St. Mary's College of Maryland, and Kevin E. Omland, University of Maryland Baltimore County, "Incomplete song divergence between the recently diverged Orchard and Fuertes' orioles."

Amanda Hagstrom, Michele Stretch, and Letitia Reichart, University of Nebraska Kearney, "Effects of handling time on corticosterone production in Red-winged Blackbird (*Agelaius phoeniceus*) nestlings."

Angelina Haines, Randolph College, "Comparison of group sizes in American Crows (*Corvus brachyrhynchos*) and Fish Crows (*Corvus ossifragus*) in suburban and rural environments."

Rachel M. Hebert, L. Scott Johnson, Allison Allen, and Felicia M. Napolillo, Towson University, "The process of fledging in the Mountain Bluebird (*Sialia currucoides*)."

M. D. Hillman, S. M. Karpanty, and J. D. Fraser, Virginia Tech, Blacksburg, "Effects of camera monitoring on Least Tern nest success at Cape Lookout National Seashore, North Carolina."

Kelsi Hunt, Nuray Taygan, Daniel Catlin, Joy Felio, and James Fraser, Virginia Tech, "Demography of Snowy Plovers (*Charadrius nivosus*) on the Missouri River."

Robert Isdell and Matthias Leu, College of William & Mary, "Factors influencing shrubland bird habitat use on the wintering grounds in the southwestern U.S."

Douglas A. James, University of Arkansas, and Ragupathy Kannan, University of Arkansas Fort Smith, "Range expansion across Arkansas by the Eurasian Collared-Dove."

Vitek Jirinec, Matthias Leu, and Daniel A. Cristol, College of William & Mary, "Does white-tailed deer (*Odocoileus virginianus*) browsing affect forest songbird communities?"

Todd E. Katzner, Philip J. Turk, Adam E. Duerr, and Tricia A. Miller, West Virginia University, Michael J. Lanzone, Cellular Tracking Technologies, Jeff L. Cooper, Virginia Department of Game and Inland Fisheries, David Brandes, Lafayette College, and Junior A. Tremblay and Charles Maisonneuve, Ministere des Ressources naturelles et de la Faune, Quebec, "Subsidized lift in migratory flight of Golden Eagles."

Evan Kelemen and Robert Curry, Villanova University, "Singing behavior in Carolina Chickadees (*Poecile carolinensis*) is consistent across contexts."

Daniel Klem, Jr., and Peter G. Saenger, Muhlenberg College, "Preventing bird-window collisions: importance of UV and other select visual signals, testing method, and window surface."

Megan Kobiela, College of William & Mary, "Does mercury contamination affect risk-taking behaviors? Tradeoffs between eating and being eaten."

Marjorie Liberati, The Ohio State University, Adam K. Janke, South Dakota State University, Mark J. Wiley, Ohio Department of Natural Resources, and Robert Gates, The Ohio State University, "Population dynamics and habitat selection of Northern Bobwhites in Ohio."

Bernard Lohr, University of Maryland Baltimore County, and Sarah M. Wakamiya, Northern Great Plains Inventory and Monitoring Program, National Park Service, "The function of song components in the Grasshopper Sparrow (*Ammodramus savannarum*)."

Ashley Love, Sarah Foltz, Ignacio Moore, and Dana Hawley, Virginia Tech, "Changes in baseline corticosterone levels in House Finches (*Haemorhous mexicanus*) during the course of infection with the naturally-occurring bacterium *Mycoplasma gallisepticum*."

Sarah A. (Manor) Luttrell, University of Maryland Baltimore County, "The call repertoire of the Marsh Wren (*Cistothorus palustris*)."

Ari Martinez and Juan Pablo Gomez, University of Florida, "Are mixed-species bird flocks stable through two decades?"

Olga Milenkaya and Jeffrey R. Walters, Virginia Polytechnic Institute and State University, "Testing the Condition-Quality Hypothesis: condition indices are repeatable but do not predict reproductive success or survival."

Adrian P. Monroe, Samuel K. Riffell, James A. Martin, L. Wes Burger, Jr., and Holly T. Boland, Mississippi State University, "Effects of vegetation structure and weather on Dickcissel nest survival in grazing systems."

Jessica Murray, Claire Ramos, Dan Cristol, and Margaret Saha, College of William & Mary, "The effect of mercury on neural gene expression during Zebra Finch development and song learning."

Felicia Napolillo, L. Scott Johnson, Rachel Hebert, Dovid Kozlovsky, and Allison Allen, Towson University, "Variation in incubation effort during egg-laying in the Mountain Bluebird and its association with hatching asynchrony."

Morgan Niccoli and Dr. Matthias Leu, College of William & Mary, "Are occupancy models feasible alternatives to collecting breeding data?"

Emily Patton Smith, Randolph College, "Preparing and utilizing natural history collections for biodiversity studies."

Jessica Pouder and Matthias Leu, College of William & Mary, "Are human footprint models an adequate tool to predict the effects of human stressors on ecological processes?"

Claire Varian Ramos, John P. Swaddle, and Daniel A. Cristol, College of William & Mary, "Genetic variation in the effects of mercury on reproduction in Zebra Finches."

Christina Riehl, Harvard University, "Cheaters and collaborators: the evolution of conspecific brood parasitism in a cooperatively breeding bird."

Gabrielle Robinson and Gary Mills, University of Georgia, Sara Schweitzer, North Carolina Wildlife Resources Commission, and Sonia Hernandez, University of Georgia, "Health and reproductive effects of mercury and PCB exposure on Least Terns."

Peter Samas and Tomas Grim, Palacky University, and Mark E. Hauber, City University of New York, "Repeatability of antiparasitic behaviors across various temporal scales."

Jennifer Scales and Melissa Hughes, College of Charleston, and Jeremy Hyman, Western Carolina University, "Fortune favors the aggressive: territory quality and behavioral syndromes in Song Sparrows."

Douglas H. Shedd, Randolph College, "Post-fledging population numbers and habitat use in the Red-billed Chough (*Pyrrhocorax pyrrhocorax*) on Valentia Island, County Kerry Ireland."

Christine Sheppard, American Bird Conservancy, "Dichotomous testing of patterns on glass provides a quantitative measure of effectiveness in reducing bird collisions."

Fletcher Smith, Bryan Watts, and Elizabeth Mojica, College of William & Mary and Virginia Commonwealth University, Jennie Rausch and Lisa Pirie, Canadian Wildlife Service, Barry Truitt, The Nature Conservancy, Tim Keyes, Georgia Department of Natural Resources, and Brad Winn, Manomet Center for Conservation Sciences, "A newly discovered migration route of the Whimbrel (*Numenius phaeopus*)."

Jessica Lynn Spickler, College of William & Mary, "Effects of sublethal methylmercury exposure on pigmented coloration in a model songbird."

Scott Stoleson and Todd Ristau, U.S.F.S. Northern Research Station, and Tim Nuttle and Ellen Yerger, Indiana University of Pennsylvania, "Ghosts of herbivory past: legacy effects of white-tailed deer on forest birds communities."

Michele Stretch, Amanda Hagstrom, and Letitia M. Reichart, University of Nebraska Kearney, "Comparison of baseline levels of corticosterone between male and female nestling Red-winged Blackbirds."

Caz M. Taylor and Andrew Laughlin, Tulane University, "Migratory flow network models: predicting the movements of migratory birds."

Robert Taylor and Mark E. Deutschlander, Hobart and William Smith Colleges, "Energetics and orientation in an irruptive migrant, the Black-capped Chickadee *Poecile atricapillus*."

Brian K. Trevelline and Brady A. Porter, Duquesne University, and Steven C. Latta, National Aviary, "DNA barcoding as a tool for the identification of prey in the feces of Louisiana Waterthrush (*Seiurus motacilla*)."

Courtney Turrin and Bryan D. Watts, College of William & Mary and Virginia Commonwealth University, "Intraspecific territorial intrusion by Bald Eagles: breeding pair response and potential effects on reproductive success in the Chesapeake Bay."

Todd J. Underwood, Kutztown University, and Spencer G. Sealy, University of Manitoba, "Bird entanglements in burdock burrs: review of a fatal attraction."

Cassie Volker and Lindsey Walters, Northern Kentucky University, "Continuous remote monitoring of nest attendance by incubating female Carolina Chickadees."

George E. Wallace and Chris Farmer, American Bird Conservancy, Sheldon Plentovich, U.S. Fish and Wildlife Service, and Holly Freifeld, Robby Kohley, Cameron Rutt, and John Vetter, American Bird Conservancy, "Successful translocation of Nihoa Millerbirds to Laysan Island, Northwestern Hawaiian Islands."

Jeffrey R. Walters, Virginia Polytechnic Institute and State University, "Alternative pathways to breeding status in the cooperatively breeding Red-cockaded Woodpecker."

Maria Wheeler and Brady Porter, Duquesne University, and Todd Katzner, West Virginia University, "The genetic impact of translocations and reintroduction: a tale of two eagles."

Douglas W. White and E. Dale Kennedy, Albion College, "Non-incubation behaviors in incubating House Wrens."

Margaret Whitney, College of William & Mary, "Depuration of and recovery from methylmercury in European Starlings."

David A. Wiedenfeld and Michael Parr, American Bird Conservancy, "Lack of information on seabird bycatch."

Michael D. Wilson, College of William & Mary and Virginia Commonwealth University, "Response of Chuck-will's-widows to fire, silviculture, and landscape configuration."

Stephanie G. Wright and Douglas A. Nelson, The Ohio State University, and Robert L. Curry, Villanova University, "Ward revisited: variation in Carolina Chickadee song across its range."

POSTERS

Amanda E. Arredondo, Sarah Baillie, and Robert Curry, Villanova University, "Effect of mate loss on breeding dispersal of chickadees."

Ashveen Bains, Valentina Ferretti, and Robert L. Curry, Villanova University, "Variation in DRD4, a gene associated with temperament, in Carolina and Black-capped chickadees."

Rachel Bellis, Baldwin Wallace University, and James Marshall, Rockford College, "Age ratios, condition, and productivity of Lake Erie islands breeding birds."

Jessica Benson, John Swaddle, and Daniel Cristol, College of William & Mary, "Mercury exposure results in hyperactivity and decreased neophobia in Zebra Finches."

Andrea Blowers, Kyle Ford, Sara Scanga, and Joel Ralston, Utica College, "Local and landscape-scale habitat characteristics of five boreal bird species."

Makayla L. Boyd, Todd J. Underwood, and Daniel F. Aruscavage, Kutztown University, "An experimental test of the effectiveness of cleaning bird feeders in winter."

R. Jory Brinkerhoff, Erin N. Lane, and Inaayat Wazir, University of Richmond, Maren Gimpel, Chester River Field Station, and Henry M. Streby, Minnesota Cooperative Fish and Wildlife Unit, "Life history characteristics of birds influence patterns of tick parasitism."

W. P. Brown and M. E. Zuefle, Keuka College, and T. J. Underwood, A. L. Alexander, and D. A. Alexander, Kutztown University, "Estimating ages of House Wren nestlings using digital images."

Luke K. Butler, College of New Jersey, "Effects of Hurricane Irene on molting chickadees."

Michael Carlo, Andrew Dolby, Deborah O'Dell, and Abigail Kimmitt, University of Mary Washington, "Effect of handling time on corticosterone and heat shock protein 60 levels in Tufted Titmouse (*Baeolophus bicolor*)."

Stephanie Cervino, College of New Jersey, and David F. Westneat, University of Kentucky, "Nestling provisioning varies with nest age, parental sex, and patch quality in the House Sparrow."

Jason Courter, Taylor University, and Gary Ritchison, Eastern Kentucky University, "Asymmetries in mobbing behavior among nuclear flockmates."

Robert L. Curry, Evan Kelemen, and Karen J. Zusi, Villanova University, and Stephanie J. Wright, The Ohio State University, "Repertoire size of Carolina Chickadee: opportunity for multi-institutional collaboration."

Tess Curry and John Swaddle, College of William & Mary, Kathleen Riley, Sam Lantz, and Jordan Karubian, Tulane University, and Mike Webster, Cornell University, "Fire history and invasive grasses change the acoustic environment of Red-backed Fairy-wrens (*Malurus melanocephalus*): implications for vocal signaling."

Kyle Davis, Big Walnut High School, Sunbury, Ohio, and Edward H. Burtt, Jr., Ohio Wesleyan University, "Size variation with altitude in the Rufous-Collared Sparrow."

Katherine Freeman, Christine Eldredge, and Robert L. Curry, Villanova University, "Black-capped Chickadee (*Parus atricapillus*) irruptions across North American from 1960–2011."

Mary Greathouse, Megan Kobiela, and Claire

Ramos, College of William & Mary, "The effect of mercury on take-off and flight in Zebra Finches."

Ankita Hanmiah, Megan Lindauer, Jennifer Rausch, and Sara R. Morris, Canisius College, "Do warblers give more flight calls with a light stimulus?"

Katie Henry and Eric Bradley, College of William & Mary, "Zebra Finch liver enzyme activity related to mercury dose."

Samantha Higgins and Kerri Cornell Duerr, Westminster College, "Do House Sparrows adjust parental care behaviors when mates desert? A test of the Negotiation Rule."

Nathan Hillis and Timothy O'Connell, Oklahoma State University, "Nest success of Western Kingbird on a university campus."

Mitchell Hinton, Annie Bendelow, Samantha Lantz, and Jordan Karubian, Tulane University, Tina W. Wey, University of California Davis, and Lee Schoen and Robin Brockett, Audubon Nature Institute, New Orleans, "Patterns of aggression among captive American Flamingos (*Phoenicopterus ruber*)."

Sydney Hope, Frank Stabile, and Luke K. Butler, College of New Jersey, "Songbird molt dynamics in fragmented and urbanized landscapes."

Aymen Hussein and Bernard Lohr, University of Maryland Baltimore County, and Brian Rolek, Archbold Biological Station, "Song characteristics of the critically endangered Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*)."

Alexandra Igo and Jameson F. Chace, Salve Regina University, "Value of urban riparian corridors as migratory stopover habitat."

Joseph R. Jehl, Jr., Brian K. Schmidt, and Christina Gebhard, U.S. National Museum of Natural History, "The spectacular migration of Eared Grebes that has never been seen: a ghost of the Passenger Pigeon."

Brittany Jones, Zachary Holtkamp, and Lindsey Walters, Northern Kentucky University, "Bird blow flies have no effect on the reproductive success of Carolina Chickadees (*Poecile carolinensis*)."

Ki Jung, Mary Willard, and Bernard Lohr, University of Maryland Baltimore County, "Song patterning, organization, and output in the Grasshopper Sparrow (*Ammodramus savannarum*)."

Cody Kent, Jack Stenger, and Edward H. Burtt, Jr., Ohio Wesleyan University, "Expanded data emphasize the importance of feather-degrading bacilli to the evolution of plumage color and maintenance behavior."

Jaan R. Kolts and Susan B. McRae, East Carolina University, "Radio-tracking King Rails in northeastern North Carolina."

Samantha Lantz and Jordan Karubian, Tulane University, "The effects of social organization on sexual selection in *Malurus* fairy-wrens."

Caleb Lemmo, Kelsey Flowers, and Sarah Mabey, Hiram College, "Phenology of songbird reproduction and seasonal arthropod abundance."

Ghazi Mahjoub, John Swaddle, Kayla Schoch, Mark Hinders, Eric Dieckman, and Elizabeth Skinner, College of William & Mary, "Can we use a sound net to block vocal communication and persistently exclude European Starlings from food sources?"

Jonathon M. Marioneaux and Jessica H. Ebers, College of William & Mary, "Temporal pattern of infection by an *Isospora* coccidian parasite of Zebra Finches."

Amanda L. McKenna, Kelsey A. Low, and Robert L. Curry, Villanova University, "Variation in plumage brightness in hybridizing chickadees and implications for mate choice."

Alexandra L. Muehlbronner, Drew G. Chernisky, and Jameson F. Chace, Salve Regina University, "Prevalence of malaria blood parasites in temperate, non-migratory birds across an urban gradient."

Oliver Muellerklein, Pavan Vutukur, and Bernard Lohr, University of Maryland Baltimore County, "Territoriality and spatial dynamics in Grasshopper Sparrows: a mathematical model."

Christina Moore and Eric Bradley, College of William & Mary, "The effect of methylmercury on plasma corticosterone concentration in Zebra Finches."

Timothy O'Connell, Monika Burchette, and Emily Clark, Oklahoma State University, "Lessons from a literal migrant trap: bird collisions on a university campus."

Karan Odom and Kevin Omland, University of Maryland Baltimore County, and Jordan Price, St Mary's College of Maryland, "Ancestral state reconstruction and life history correlates of duetting in the New World blackbirds."

Kelly E. O'Toole, College of William & Mary, Kathryn Grabenstein, Cornell University, Mitchell G. Hinton, Tulane University, John P. Swaddle, College of William & Mary, Jordan Karubian, Tulane University, and Michael S. Webster, Cornell University, "Habitat preference of a tropical passerine in a fire-prone environment."

Langbo Ou, Claire W. Varian Ramos, and Daniel A. Cristol, College of William & Mary, "Temporal pattern of mortality in Zebra Finch nestlings exposed to methylmercury."

Davia Palmeri and Wayne Law, Columbia University and The New York Botanical Garden, "Impacts of sakau cultivation on the upland forest bird diversity of Pohnpei, Federated States of Micronesia."

Rachel Porter, Rebecca Simmons, and Jameson F. Chace, Salve Regina University, "Impacts of the urban environment on stress hormone corticosterone level in Black-capped Chickadees and Tufted Titmice."

John E. Quinn, Furman University, "Conservation of Bell's Vireo in agroecosystems."

Abbey Ramirez and Timothy O'Connell, Oklahoma State University, "Habitat selection of nesting Mississippi Kites in Oklahoma Cross Timbers."

Claire Varian Ramos, Zoe S. Welch, Jessica R. Murray, and Margaret S. Saha, College of William & Mary, "Embryological staging of the Zebra Finch, *Taeniopygia guttata*."

Bishoy S. Saleeb, Daniel C. Miller, and Sara R. Morris, Canisius College, "Is there a seasonal difference in flight call responses by warblers?"

Kathryn J. Schneider, Hudson Valley Community College, and Jeremy J. Kirchman, New York State Museum, "Three long term data sets detail accelerating range expansion and the breakdown of Bergmann's Rule in Red-bellied Woodpeckers (*Melanerpes carolinus*)."

Sheila Scoville, Eastern Virginia Medical School, and Claire Ramos and Daniel Cristol, College of William & Mary, "Mercury impairs cerebellar development in Zebra Finches (*Taeniopygia guttata*)."

Chad L. Seewagen, AKRF Inc. and Pace University, "Mercury exposure and the stopover refueling performance of migrating Northern Waterthrushes."

Shailee Shah and David Bonter, Cornell University, "Communication of threat-level in alarm calls of Herring Gulls (*Larus argentatus*)."

Benjamin Skolnik, American Bird Conservancy, and Heidy Valle, Fundación ProAves, "Dusky Starfrontlet and Antioquia Antpitta: conservation planning and implementation."

Christina Slover and Todd Katzner, West Virginia University, "Impacts of prescribed burning on avian community structure in the Central Appalachians."

Eliza Spear, Mitch T. Caudill, and Claire Varian-Ramos, College of William & Mary, "Effects on immune response of lifelong or adult exposure to mercury in Zebra Finches."

Frank Stabile, Sydney Hope, and Luke K. Butler, College of New Jersey, "Age contrasts in the timing of body molt in the Carolina Chickadee."

Samantha Stoklosa and Amanda Rodewald, The Ohio State University, "Brood parasitism on Northern Cardinals: relationship between distance to edge on early clutch initiation."

Jeff Stratford, William Biggers, Christopher Bartlow, Nathanial Lamoreaux, Kelly Rauschmeier, Anthony Pero, Katie Sceia, Timothy Hoffman, and Nipa Parikh, Wilkes University, "Relationship between land use, natural gas well density, and antioxidant activity in Pennsylvania songbirds."

Rachel G. Thomas, Edward H. Burtt, Jr., and Laura Tuhela, Ohio Wesleyan University, "Analyzing the effect of an unusual feather pigment on the resistance to bacterial feather-degradation in turacos."

Derrick Thrasher, Cornell University, and Kathryn Sieving, University of Florida, "Characteristics of breeding habitat and habitat use of the Eastern Painted Bunting in Florida."

James Ward, Colin Feeney, and Kerri Cornell Duerr, Westminster College, "Effects of Marcellus Shale natural gas wells and land use on post-breeding raptor populations in southwest Pennsylvania."

Emily Webb and Amanda Fawcett, Ohio Wesleyan University, "Pattern of occurrence of porphyrins in avian eggshells."

Kaylor Wright, Claire Ramos, Jessica Spickler, Nelson Wu, Molly Ross, and Eric Bradley, College of William & Mary, "No effect of low-dose mercury exposure on plasma testosterone in developing and reproducing male Zebra Finches."

ATTENDANCE

ARIZONA: *Tucson,* Clait E. Braun, Nancy J. K. Braun.

ARKANSAS: *Fayetteville,* Elizabeth Adam, Douglas A. James.

CONNECTICUT: *New Britain,* Sylvia Halkin.

DISTRICT OF COLUMBIA: Faridah Dahlan, Carla J. Dove, Marcy Heacker, Storrs L. Olson, Benjamin Skolnik, George E. Watson, James Whatton.

FLORIDA: *Gainesville,* Ari Martinez; *Naples,* Bette Jackson, Jerome A. Jackson; *Tampa,* Erin Feichtinger.

GEORGIA: *Athens,* Gabrielle Robinson.

ILLINOIS: *Rockford,* James Marshall.

INDIANA: *Notre Dame,* Doris J. Watt; *South Bend,* Melinda M. Clark, Kerri Martin; *Upland,* Jason Courter.

KENTUCKY: *Highland Heights,* Zachary Holtkamp, Brittany Jones, Cassie Volker, Lindsey Walters.

LOUISIANA: *New Orleans,* Mitchell Hinton, Samantha Lantz, Kathleen Riley, Caz M. Taylor.

MARYLAND: *Annapolis,* Joseph R. Jehl, Jr.; *Baltimore,* Aymen Hussein, Ki Jung, Archer Larned, Bernard Lohr, Sarah Luttrell, Oliver Muellerklein, Karan Odom; *Chestertown,* Maren Gimpel; *Chevy Chase,* Ellen Paul; *Fredericksburg,* Johanna Humphrey; *Silver Spring,* Hellen Patton; *Towson,* Rachel Hebert, L. Scott Johnson, Felicia Napolillo.

MASSACHUSETTS: *Cambridge,* Christina Riehl; *Chestertown,* Daniel Small; *Concord,* Jeff King; *East Falmouth,* Betsy Davis, William E. Davis, Jr.; *Pocasset,* John C. Kricher, Martha Vaughn.

MICHIGAN: *Albion,* E. Dale Kennedy, Douglas W. White; *Port Huron,* David Webb.

MISSISSIPPI: *Mississippi State,* Adrian Monroe.

MISSOURI: *Bolivar,* Dennis G. Siegfried.

NEBRASKA: *Kearney,* Amanda Hagstrom, Letitia M. Reichart, Michele Stretch; *Lincoln,* Mary Bomberger Brown.

NEW JERSEY: *Ewing,* Luke K. Butler, Stephanie Cervino, Sydney Hope, Frank Stabile; *Princeton,* Peter Grant, Rosemary Grant; *Randolph,* John A. Smallwood, Mary Anne Smallwood.

NEW YORK: *Albany,* Alyssa FitzGerald, Jeremy Kirchman; *Buffalo,* Corey Callaghan, Kaitlin Garrity, Ankita Hanmiah, Megan Lindauer, Daniel Miller, Sara R. Morris, Jennifer Rausch, Bishoy Saleeb; *Floral Park,* Davia Palmeri; *Geneva,* Mark E. Deutschlander; *Hempstead,* MaryAnn Boyce, Maureen Boyce; *Ithaca,* Caleb Arellano, Daniel Baldassarre, Kathryn Grabenstein, Shah Shailee, Derrick Thrasher; *Keuka Park,* William Brown; *New York,* Mark E. Hauber; *Pelham,* Christine Sheppard; *Rockville Center,* Todd Russo; *Utica,* Andrea Blowers, Kyle Ford, Joel Ralston.

NORTH CAROLINA: *Chapel Hill,* Helmut Mueller, Nancy Mueller; *Greenville,* Carol Brackett, Jaan Kolts, Susan McRae; *Raleigh,* Jeanne Conner, Richard N. Conner; *Wilmington,* Rebecka Brasso.

OHIO: *Berea,* Rachel Bellis; *Brunswick,* Emity Slee; *Columbus,* John Lennon, Marjorie Liberati, Samantha Stoklosa, Stephanie Wright; *Delaware,* Edward H. Burtt, Jr., Kyle Davis, Cody Kent, Rachel Thomas, Emily Webb; *Hiram,* Caleb Lemmo, Sarah Mabey; *Sandusky,* Robert C. Beason.

OKLAHOMA: *Stillwater,* Nathan Hillis, Timothy J. O'Connell, Abbey Ramirez, Shen Ramirez.

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